GENERAL BOTANY

WITH SPECIAL REFERENCE TO ITS ECONOMIC ASPECTS

Digitized by the Internet Archive
in 2026 with funding from
University of Toronto

https://archive.org/details/generalbotanywit00gage

Bot.
G.

GENERAL BOTANY

WITH SPECIAL REFERENCE TO ITS ECONOMIC ASPECTS

TORONTO

BY

C. STUART GAGER, Ph.D., Sc.D., Pd.D.

DIRECTOR OF THE BROOKLYN BOTANIC GARDEN, AUTHOR OF FUNDAMENTALS OF BOTANY, LABORATORY GUIDE TO GENERAL BOTANY, HEREDITY AND EVOLUTION IN PLANTS, ETC.

WITH THREE CHAPTERS ON

HEREDITY AND VARIATION IN PLANTS

BY

ORLAND E. WHITE, Sc.D.

CURATOR OF PLANT BREEDING AND ECONOMIC PLANTS, BROOKLYN BOTANIC GARDEN

WITH 689 ILLUSTRATIONS

207737
21. 12. 26

PHILADELPHIA

P. BLAKISTON'S SON & CO.

1012 WALNUT STREET

1926

Copyright, 1926, by P. Blakiston's Son & Co.

PRINTED IN U. S. A.
BY THE MAPLE PRESS COMPANY, YORK, PA.

TO

MY WIFE

BERTHA BAGG GAGER

PREFACE

There is a vast difference between educating one to be a scientist and the education of scientists. The former takes account chiefly of the occupation in which a man is to engage as a life-work; the latter takes account of the man. One is a better scientist if he is not *merely* a scientist, just as one is a better lawyer, farmer, merchant, preacher, if he is more than his calling.

Education, whether for a profession or primarily for culture, as in the liberal arts colleges, should always regard the individual and society as of primary importance. The average man or woman devotes to his calling not more than eight or ten hours a day, six days a week; he has to live with himself and with others twenty-four hours a day, seven days a week. Obviously the first aim of all education should be to fit one to live; its second aim, to fit one to earn a living.

If these considerations are valid, what should be the content and method of instruction of the various studies that make up the curriculum in our universities and colleges? It would seem self-evident that the method of instruction should be such as to give the student an understanding of scientific method, and some considerable exercise in the use of it. He should also be made to realize that the method of science is the only method by which he can hope to arrive at a correct understanding of himself and his environmnet, so that he may make a proper adjustment thereto. Maladjustment spells failure.

The student will learn that scientific method includes, among other things, accurate observing and recording of facts, their painstaking analysis and classification, the drawing of strictly logical inferences based upon the evidence in hand, the rigid testing of his inferences, and acceptance of the necessary conclusions, however much they may be contrary to his hopes, or his preconceived ideas, or his prejudices. He will learn the distinction between fact and hypothesis, and how to employ the

method of the working hypothesis. In facing the major problems of life the great need is not so much to know *what* to think, but *how* to think.

As to the content of the first course of study in botany, it is by no means self-evident that this should be greatly different for students in an agricultural college, expecting to make some line of agriculture or horticulture their life work, than for students preparing for any other vocation. It is important for both groups that the content of the course shall have cultural value as well as informational value. As a recent educational writer has well said, a specialist should show that he is *educated* in a specialty, and not merely that he has specialized in a given occupation or branch of knowledge. If, from the first course of botany, the prospective agriculturist gets only certain information which has a more or less immediate application in agricultural practice he has been impoverished where he might have been enriched, and the college has failed to discharge its most important duty to its students.

A subject has cultural value in proportion to the number of human contacts it gives the pupil, the extent to which it broadens his views and extends his interests and sympathies. A recent book is entitled "The Humanizing of Knowledge." This is a crying need in all science teaching—elementary and advanced. It has for long been argued that in botany the student should be made to realize how intimately his own life is bound up with the life of plants, and yet he has been given to study wild flowers which he may never have seen and has little to do with, while nothing is said of dates, cotton, flax, corn, wheat, rice, and numerous other cultivated plants which have profoundly affected the beginnings of civilization, the course of human history, and his own daily life. Or if these plants are studied it is chiefly their structure; little is said of their place and importance in human history.

From the same consideration the present book, while intended primarily for use in the United States of America, includes discussions of economic plants not cultivated in the States, since one can hardly consider himself *educated* in agriculture who is ignorant of the crop plants of other countries than his own.

Few who study introductory courses in any science have any realization of how the human race came into the possession of this precious heritage of knowledge. Facts are so often presented as if they had no history, or as if they had always been known. We even take for granted the very names of plants. How wonderful it is that they are all named! Someone, of course, named them. Every known item of knowledge had its discoverer, its first time and place of publication, and its subsequent history involving modifications and revisions, especially in the direction of greater accuracy of statement.

Technical terms should not be imposed on the student as mere arbitrary handles of ideas. There is often as much education in learning the meaning or history of a scientific term as in learning its definition. It is much more interesting and instructive to know why the pistil of a flower is so named than merely to be able to utter the word at the proper time. These things should all be included in the student's introduction to the science. If these things were not disregarded we should hear less of the futile discussion about the relative cultural value of the sciences and the "humanities;" the sciences would become humanities.

Some introductory texts appear to be written on the supposition that the pupil is interested in advance, but it should be one of the chief obligations of the teacher so to present the subject matter in the first course as to arouse interest where lacking and to deepen whatever interest the pupil may already possess.

One other mistake of the first order is to proceed on the supposition that the main purpose of the first course is to prepare the pupil for advanced courses. Nothing could be more erroneous. Many students take a first course in a given science merely because it is a required course, still others elect the course for the purpose of ascertaining what the given subject is like, to find out whether they are or are not interested in that subject—whether it has any meaning for them. The student who, at the completion of the first course in any subject, finds that his major interest lies elsewhere, is to be congratulated as cordially as the student who finds to the contrary. One of the chief purposes served by all introductory courses is to enable students to discover where their major life interest does lie, and the first course should have such a content and method of presentation

as to make every student, at the end, feel that the course has been interesting and profitable, whether he pursues the subject further or not. A course planned with reference to this broader aim should prove to be entirely satisfactory as a foundation for more advanced courses.

The present book has been prepared on the supposition that a foundation for reading the text will be laid in thorough laboratory work. Many facts that will be learned at first hand in the laboratory have been purposely omitted here. On the other hand an attempt has been made to enrich the text with interesting information of educational value, not always, perhaps, strictly botanical (in the narrow sense of the term), but intimately related to the plant or to the botanical subject being discussed. Commercial and other statistics have, for the most part, been intentionally omitted. They might properly be included in a course in Commercial Geography. The aim has been to show that plant life has been, throughout history, and still is closely interwoven with human life.

Chapters XL–XLII have been written by Dr. Orland E. White, Curator of plant breeding and economic botany, Brooklyn Botanic Garden. Dr. White has done the author the great service of critically reading the entire manuscript. Dr. George M. Reed, curator of plant pathology, Brooklyn Botanic Garden, has also been good enough to read the manuscript of Chapters XXII and XXIV, and parts of other chapters. Dr. Alfred Gundersen, also curator in the same institution, has given valuable criticism of the nomenclature and other points, and is co-author of Chapter XXVII. The author is under great obligations to Dr. Arthur Harmount Graves, curator, Brooklyn Botanic Garden, who has rendered the invaluable service of reading the entire proof. While the text has greatly profited by these services, the author alone is responsible for all errors and omissions.

The author is deeply indebted to numerous individuals and institutions for photographs reproduced as half-tones, and to publishers and authors for permission to reproduce illustrations, as follows:

Dr. Charles O. Appleman and the Maryland Agricultural Experiment Station for numerous figures credited to Appleman in the legends; P. Blakiston's Son & Co., and to Profs. W. W.

Robbins and W. C. Stevens, for loan of cuts and permission to reproduce the various illustrations credited in the legends to the respective authors; D. Appelton & Co., New York, Figs. 648–650; Dr. N. L. Britton and Charles Scribner's Sons, Figs. 400, 402, 403, 426, 551, 554–556, 570; Prof. A. H. Reginald Buller, Figs. 346, 360, 361; Prof. D. H. Campbell and the MacMillan Co., Fig. 317; Prof. W. E. Castle and the Journal of Heredity, Fig. 683; Mr. Arthur H. Church and the Clarendon Press, Figs. 461–462; J. & A. Churchill, Fig. 10; Prof. F. E. Clements and Henry Holt & Co., Fig. 42; Prof. C. C. Curtis and Henry Holt & Co., Fig. 324; Doubleday, Page & Co., Fig. 272; Prof. Donald Folsom and Director W. J. Morse, Main Agricultural Experiment Station, for the photographic print reproduced as Fig. 518; Prof. William F. Ganong and Henry Holt & Co., Figs. 52, 94; Henry Holt & Co., Figs. 158, 314–316; Jones & Rayner and Methuen & Co., Fig. 144; Prof. T. A. Kiesselbach and Nebraska Agricultural College, Figs. 263 and 264; Prof. Francis E. Lloyd, Fig. 326; Prof. J. P. Lotsy and Gustav Fischer, Fig. 664; Messrs. Peabody and Hunt and The MacMillan Co., Fig. 47; Mr. John Percival and Gerald Duckworth & Co., Ltd., Figs. 138, 245, 433, 510, 511; Public Photo Service Inc., Fig. 58; Pres. George C. Roeding of Faucher Creek Nurseries, Fresno, Calif., Fig. 399; Dr. Albert Schneider and Willard N. Clute & Co., Fig. 124; Mr. J. Marion Shull and The Journal of Heredity, Fig. 74; Prof. W. C. Stevens and D. C. Heath & Co., Figs. 277–278; U. S. Department of Agriculture, for numerous illustrations acknowledged in their legends; Wild Flower Preservation Society of America (through Mr. P. L. Ricker, Secretary), Fig. 177; Prof. R. H. Yapp and the University Press, Cambridge (England), Figs. 70, 71, 73.

The pen drawings for figures 140, 231, 232, 238 and 252, were made by Mr. William W. Sexton; the drawings for the other original line cut illustrations were made by Miss Maude L. Purdy.

Most of the half-tone illustrations in this book, when not otherwise credited, have been reproduced from photographs made by Mr. Louis Buhle, photographer at the Brooklyn Botanic Garden. Such clearness as they possess is due in large measure to his painstaking work.

And, finally, the author wishes to act on the wise advice of Epictetus, as quoted by William Congreve in the dedication of

one of his plays. Every author, said Epictetus, should say to the critics of his work, "That if they who find some faults in it were as intimate with it as I am, they would find a great many more."

C. STUART GAGER.

BROOKLYN BOTANIC GARDEN,
July 15, 1925.

THE FUNDAMENTAL IMPORTANCE OF BOTANY

By Jean Baptiste Lamarck[1]

The science which has for its object a knowledge of plants and to which is particularly given the name Botany is, I do not hesitate to say, of all the sub-divisions of natural history, that which presents at the same time the most numerous objects of utility and the most varied charms. The wholesome foods of every kind which plants offer to man for his most essential needs, the innumerable resources that they furnish to medicine in the treatment of diseases, the multifarious tributes with which they enrich nearly every art, and finally the charms which they possess, whether in the field or in our gardens under a thousand different aspects all, in a word, concur to assure a marked pre-eminence to the study of that extensive branch of human knowledge, and to make one realize its inexhaustible attractions.

That beautiful science does not consist, as is commonly supposed, in the sterile ability to memorize by heart many names of plants and to apply the names to the plants to which they belong, but it consists in an intimate knowledge of the plants themselves, their development, their organization, their relations, the essential characters which distinguish species with constancy, the common traits which bind together certain numbers of different

[1] Lamarck. Jean Baptiste Antoine Pierre *Monnet* (Chevalier de Lamarck). Born at Bazantin, in the Somme, August 1, 1744; died in Paris December 18, 1829. Proposed one of the first comprehensive theories of organic evolution, elaborated in his *Philosophie Zoologique* (1809). Traveled through Europe as "botanist to the King" (1781–82). Keeper of the herbarium in the *Jardin du Roi* (1788). Assisted (1793) in reorganizing this royal garden into the now famous *Jardin des Plantes*, in which he was made professor. It was he who suggested the change of name in order, during the French Revolution, to eliminate the adjective Royal (*du Roi*). His botanical writings include *La Flore Francaise* (1778), *Encyclopédie méthodique Botanique* (1783–1817). *Histoire Naturelle des vegetaux*, etc., Vols. I and II (1802). In 1794 he abandoned his botanical work and became a zoologist.

plants and result in the formation of different kinds of groups, which botanists call Classes, Orders, Families, and Genera; the limits which nature has imposed on varieties, that is to say, on the different variations which circumstances have been able to bring about in plants. These different kinds of knowledge always indicate the marked difference between the botanist, who embraces them both, and the simple nomenclator.

I do not hesitate to say that the innumerable services which plants may render to man, under every possible circumstance, are never the result of a study of their virtues and their particular qualities only; one should not flatter himself that he can attain that object unless he carries on, shoulder to shoulder with that research, the study of the characters which distinguish plants and which are the only means of perpetuating the knowledge of their uses.

One finds a very convincing proof of this truth if he goes back to the more ancient times and considers the state in which botany was then. In those times, when this beautiful science was just beginning, men occupied themselves solely with its utility and took no precaution to make sure of the properties of plants which experience, or happy accident, had led them to discover. They neglected entirely the means of perpetuating their discoveries by the distinction and exact description of the plants which they had studied, and without which their success could have only a momentary and transient utility.—*Translated from Lamarck's Discours Preliminaire. Encyclopédie Méthodique Botanique.* Tom I.

CONTENTS

PART I

Introduction

Chapter		Page
I.	The Problems of Botany as Illustrated by the Clover	3–13
II.	The Cell	14–26

PART II

The Vegetative Functions of Plants

III.	The Absorption of Water and Mineral Nutrients	29–52
IV.	Loss of Water: Transpiration	53–67
V.	Transportation of Liquids	68–80
VI.	The Struggle against Drought	81–130
VII.	Fermentation	131–146
VIII.	Respiration	147–156
IX.	Nutrition	157–171
X.	Formation and Rôle of Carbohydrates	172–198
XI.	Saprophytism and Symbiosis	199-221
XII.	The Nitrogen Problem	222–244
XIII.	Growth	245–270
XIV.	Adjustment to Surroundings	271–297

PART III

Reproduction and Life-histories

XV.	Reproduction	301–331
XVI.	How Seeds Are Made	332–362
XVII.	Cross-pollination	363–405
XVIII.	Kinds and Classification of Fruit	406–409
XIX.	Interpretation of the Flower and Seed	410–425
XX.	Interpretation of the Flower and Seed (Concluded): Life History of the Pine	426–437
XXI.	Lower Cryptogams	438–459
	Life History of a True Moss	438
	Life History of a Liverwort	444
	Algae	447

Chapter		Page
XXII.	Character and Life Histories of Fungi	460–478
XXIII.	Character and Life Histories of Fungi (Concluded)	479–516
XXIV.	Economic Importance of Fungi	517–544
XXV.	The Problem of Sex in Plants	545–554

PART IV

The Great Groups of Seed-bearing Plants

XXVI.	Principles of Classification	557–563
XXVII.	Evolution and Classification	564–570
XXVIII.	The Families of Flowering Plants (Angiosperms): Apetalous and Polypetalous Dicotyledons	571–609
XXIX.	Polypetalous Dicotyledons (Continued)	610–633
XXX.	Polypetalous Dicotyledons (Continued)	634–664
XXXI.	Polypetalous Dicotyledons (Continued)	665–682
XXXII.	Polypetalous Dicotyledons (Concluded)	683–710
XXXIII.	Sympetalous Dicotyledons	711–741
XXXIV.	Sympetalous Dicotyledons (Continued)	742–775
XXXV.	Sympetalous Dicotyledons (Concluded)	776–792
XXXVI.	Monocotyledons	793–823
XXXVII.	Monocotyledons (Continued)	824–854
XXXVIII.	Monocotyledons (Continued)	855–901
XXXIX.	Monocotyledons (Concluded)	902–931

PART V

Genetics and Evolution

XL.	Heredity, Variation, and Environment	935–970
XLI.	The Physical Basis of Heredity	971–982
XLII.	Generalizations and Special Cases	983–1000
XLIII.	Evolution	1001–1012

Index 1013

PART I
INTRODUCTION

CHAPTER I

THE PROBLEMS OF BOTANY AS ILLUSTRATED BY THE CLOVER

All science is the result of curiosity. The word curiosity is derived from the Latin word *cura*, care, and is commonly used when we have a care or (as the dictionary says) an eager concern to get knowledge about unusual or unfamiliar or mysterious occurrences or things. When the knowledge sought is obtained, our curiosity is said to be satisfied. Every one, sooner or later, comes to realize that some of the things about which he is curious make a stronger appeal to him than others; he recognizes that they have special significance in connection with his ideals and aspirations, and his curiosity gives way to, or develops into, interest. One's interests may change, but we seldom, if ever, hear of one's interest being satisfied. Genuine interest is persistent, and leads one to give sustained attention to the object of his interest. He is continually seeking to know more about it. When the resulting knowledge is logically arranged or classified it becomes *science*, as distinguished from mere unrelated bits of information.

Fortunately, the interests of men vary; some are interested in color and form and become artists, others in sound and harmony and become musicians, others in the deeds of men and nations and become historians. Interest in natural objects, with a desire to understand and explain them, is characteristic of scientists; and we have astronomers, geologists, chemists, zoologists, *et cetera*, according to the class of objects in which one is interested. When the major interest of one's life is plants he becomes a *botanist*, and the classified and exact knowledge obtained by studying plants constitutes *the science of botany*. Not everyone can become sufficiently interested in plants to make him a botanist, but it is always an advantage, and often a great pleasure, to have a wide range of interests, and to be intelligent about a variety of subjects besides one's major interest or specialty.

Some who study this book may become interested in plants for their own sake, and become botanists; others will find botany only an added interest in life, while still others will, or have already, become interested in the applications of botany to horticulture or agriculture and other occupations or *applied sciences* founded in whole or in part upon the science of botany. It is primarily for the latter class that this book is prepared, for while "agricultural botany," so-called, is not essentially different from any other kind of botany—that is, the facts and principles are not different—the emphasis is placed on those phases or parts of the subject that are applied in agricultural or horticultural practice, and especially in the raising of crops of cultivated plants. The major problems of botany are concretely embodied in many flowering plants. For convenience we may choose one of the clovers for an introductory study. Clovers are of special interest to agricultural students because, from the standpoint of hay, and honey, and soil fertility they constitute one of the most important crop plants in the world, and, therefore, intimately related to our daily lives.

DESCRIPTION OF THE CLOVER PLANT

General.—The red clover (*Trifolium pratense*) is chosen as an example (Fig. 1). We observe that the part of the plant above ground consists of a *stem* with *branches*. At intervals on the stem are *leaves*, and at the tips of some of the branches are the clover "blossoms." The stem is of a greenish color, cylindrical and elongate. The branches always arise in the angle (*axis*) between a leaf and the branch that bears it. Every plant organ so situated, no matter how disguised it may be in form or structure, is a branch, and the appendages that *subtend* branches are leaves, however much they may be disguised in appearance or structure.

The Leaf.—By a more careful examination of a leaf we learn that the flat, thin, green, more or less oval (or obovate or oblong) parts are not the entire leaf; each of these parts is a *leaflet*, and three leaflets constitute the (compound) *leaf-blade*, borne on a common *leaf-stalk* or *petiole*. In exceptional cases there are four, or even 5, 7, or 9 leaflets (Fig. 2). The little stalk of each leaflet is a *petiolule*. The free end of each leaflet is the *apex*, and the opposite portion attached to the petiolule is the *base of the blade*

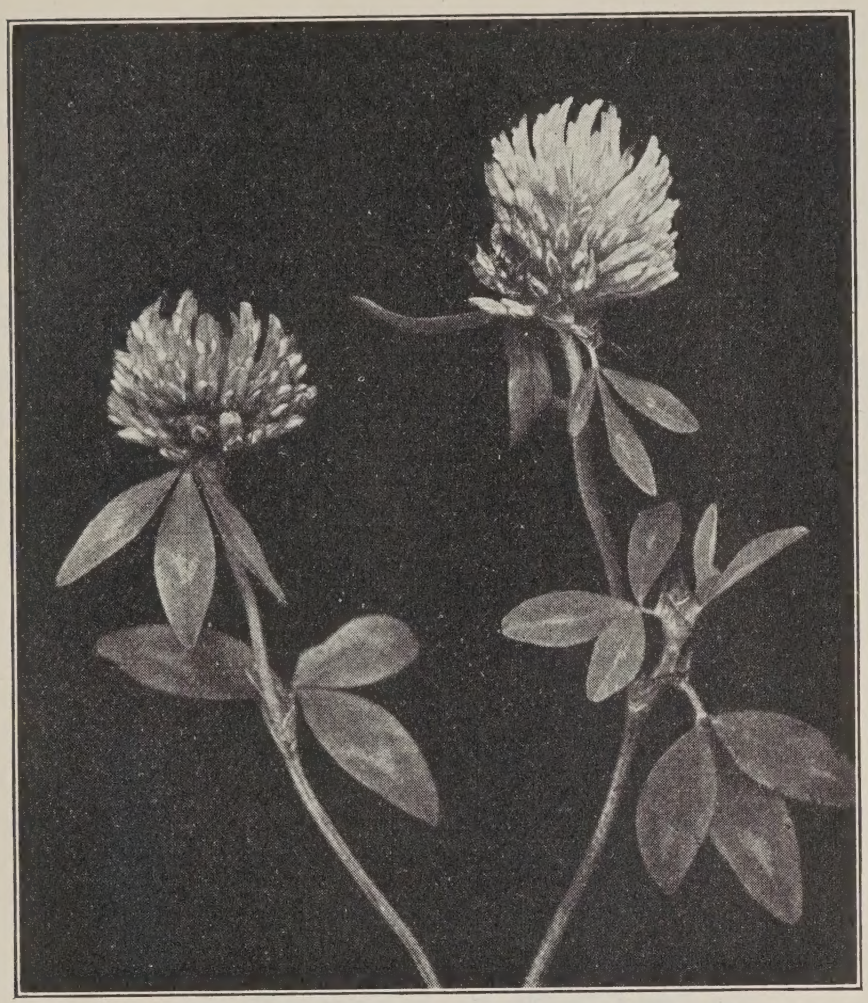


FIG. 1.—Red clover (*Trifolium pratense*). Branches showing flowers and leaves.

FIG. 2.—Clover leaves with three to nine leaflets. The normal clover leaf is *pinnately* compound, with three leaflets.

The margins are finely toothed or *serrate,* and if the leaflet is held up to the light, tiny *veins* may be seen extending in all directions, forming a network. The portion of the petiole adjoining the branch is the *leaf-base.* The membranous outgrowths of the leaf-base are *stipulse.* We also notice numerous fine *plant-hairs* on the leaf-stalk and blade, and that the upper surface of the blade is of a darker green color than the under surface. Towards night or on very cloudy days we may note that the leaflets hang downward, but resume their horizontal, expanded position on the return of sunlight.

The Blossom.—If the clover blossom is examined in detail it will be seen that it is not a simple flower, like a lily or a rose, but a

FIG. 3.—Clover "blossom" or inflorescence in longitudinal section. The lowest flowers or florets were the first to open and are now permanently closed. *pd.*, peduncle; *fl.*, floret.

flower-cluster or *inflorescence,* comprising many small flowers, or *florets,* their stalks (*pedicels*) inserted on a shortened axis or *receptacle;* this terminates a stalk called the *peduncle.* Such a flower cluster is called a *head* (Fig. 3). In very young heads are found only *flower-buds.* It is seen that the smaller and younger buds are nearer the center of the head. In older inflorescences some of the flowers have opened, and one notes that the outer-

most flowers always open first, the opening or *anthesis* progressing in toward the center (*centripetal*). Buds and fresh flowers stand erect, but older flowers begin to bend back (*reflexed*) from the center and finally hang downward, the outermost often appressed against the flower stalk. It will also be observed that the florets that are beginning to turn back are usually of a deeper color than those that have just opened; the color finally fades and the flower becomes brown and withered.

The Flower.—The individual flower (Fig. 4) is borne on a tiny stalk of its own, the *pedicel.* There are two *floral envelopes*—the

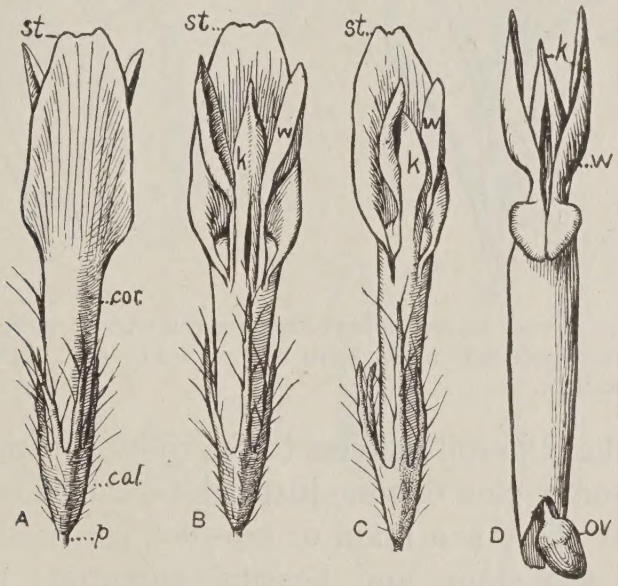


FIG. 4.—Flowers of red clover. A–D various views. *p*, pedicel; *cal*, calyx; *cor*, corolla; *st*, standard; *k*, keel; *w*, wing; *ov*, ovary. In *D* the upper part of the standard has been removed.

outer one, the *calyx*, green in color, cup shaped, and bearing five nearly equal *calyx teeth;* the inner one, the *corolla*, more conspicuous, pinkish-white, and composed of five more or less distinct parts or *petals*, as follows: a relatively large, erect, conspicuous petal, the *standard*, two anterior petals, loosely united along their margins to form a *keel*, and two lateral petals, the *wings*. In the bud the keel is enclosed by the wings, and all four of these parts are enclosed by the standard. Within the corolla are the *stamens*, each comprising an *anther* borne on a *filament* (Fig. 5). The anthers contain *pollen*. The filaments adhere throughout a portion of their length, and are in two groups (*diadelphous*) of one and nine respectively. Within the circle of stamens, and terminal on the

pedicel, is the *pistil*, composed of the basal *ovary*, and the *stigma* at the tip of the stender *style* (Fig. 6). The stamens and pistil are the *essential organs* of the flower. The stem and branches, together with the leaves and flowers, comprise the *shoot*.

The Roots.—If we proceed with care we may loosen the clover plant from the soil, so as to disclose the root system, though many of the smaller rootlets will become broken off and remain in the soil. The difficulty of removing the plant from the soil discloses one of the functions of roots, namely, to anchor the plant to the soil.

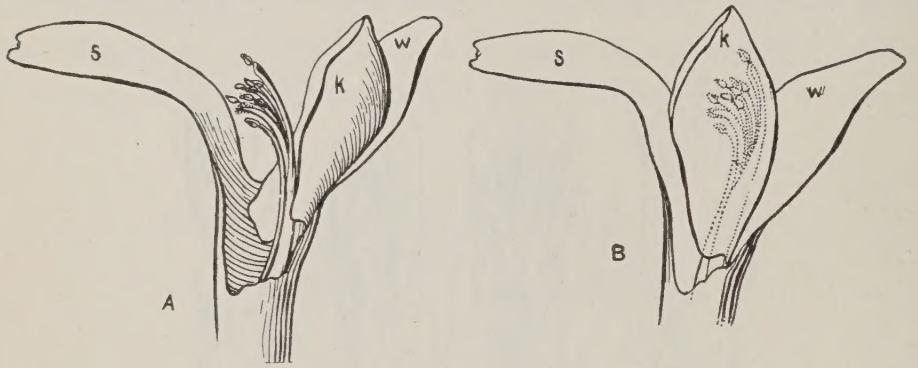


FIG. 5.—Clover flower, upper part; one wing removed. *s*, standard; *k*, keel; *w*, wing. In B the parts are in place; in A the keel is bent back to disclose the essential organs within.

We notice that the soil adheres to the roots, but mostly only to a relatively short region or zone just behind the ends of the roots. In some plants there is a main or *tap-root*, corresponding to the main axis of the stem, and bearing numerous branch roots and rootlets (Fig. 7). Among the most conspicuous features of the root system are the small nodules or *tubercles* (Fig. 8).

The Fruit.—We have now noted the principal organs of the mature plant, but there remain two very important parts which have not yet been mentioned. We have seen that the older flowers of the head become reflexed, and if we examine clover heads that are quite mature we shall find that all the parts of the reflexed flowers are withered or possibly fallen away, except the calyx and the central organ or pistil. The pistil has not only persisted, but the basal part, the ovary, has grown larger, and developed into a small pod, somewhat like a pea pod. This is the ripened ovary, and a ripened ovary is known botanically as a *fruit*. The style has withered, but persists at the tip of the pod, while the calyx persists at the other end (Fig. 6, C and D).

The Seed.—The pod usually does not open or *dehisce* of itself, or only tardily along one edge or *suture*. If we open it we shall find within about four clover *seeds*, each attached by a tiny stalk to the edge of the pod opposite the suture. The fruit

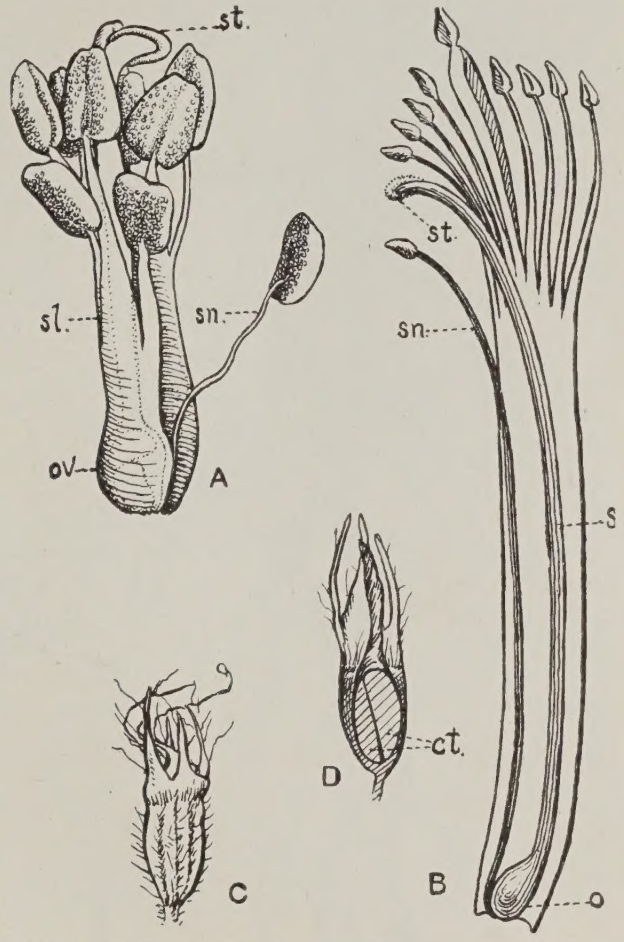


FIG. 6.—*A*, the ten diadelphous stamens from a flower-bud of clover. The nine united stamens inclose the pistil, whose stigma is shown at *st*; *s*, style; *o*, ovary. *B*, the same organs from a mature flower. *C*, calyx inclosing a ripening ovary. *D*, ripened ovary in longitudinal section showing the two halves or cotyledons (*ct*) of one of the seeds which the ovary contains.

may contain from one to six seeds. The stalk of a seed is called the *funiculus*, and the place where it is attached to the pod is the *placenta* (Figs. 9 and 237). Each seed is globular and hard, and apparently lifeless. If we examine it more thoroughly we shall find that the outer seedcoat shows a scar (*hilum*) where the funiculus was broken off, and near the scar, at one side, is a very tiny hole, scarcely visible to the naked eye. This is the *micropyle*. The seed-coat, hard in dried seeds, encloses an *embryo* of another clover plant. This embryo is composed of two thick or "fleshy"

seed leaves (the *cotyledons*), a very tiny peg, the *hypocotyl*, which is the beginning of the stem, lying with its tip directly under the micropyle, and the first bud or *plumule* at the end of the hypocotyl between the cotyledons.

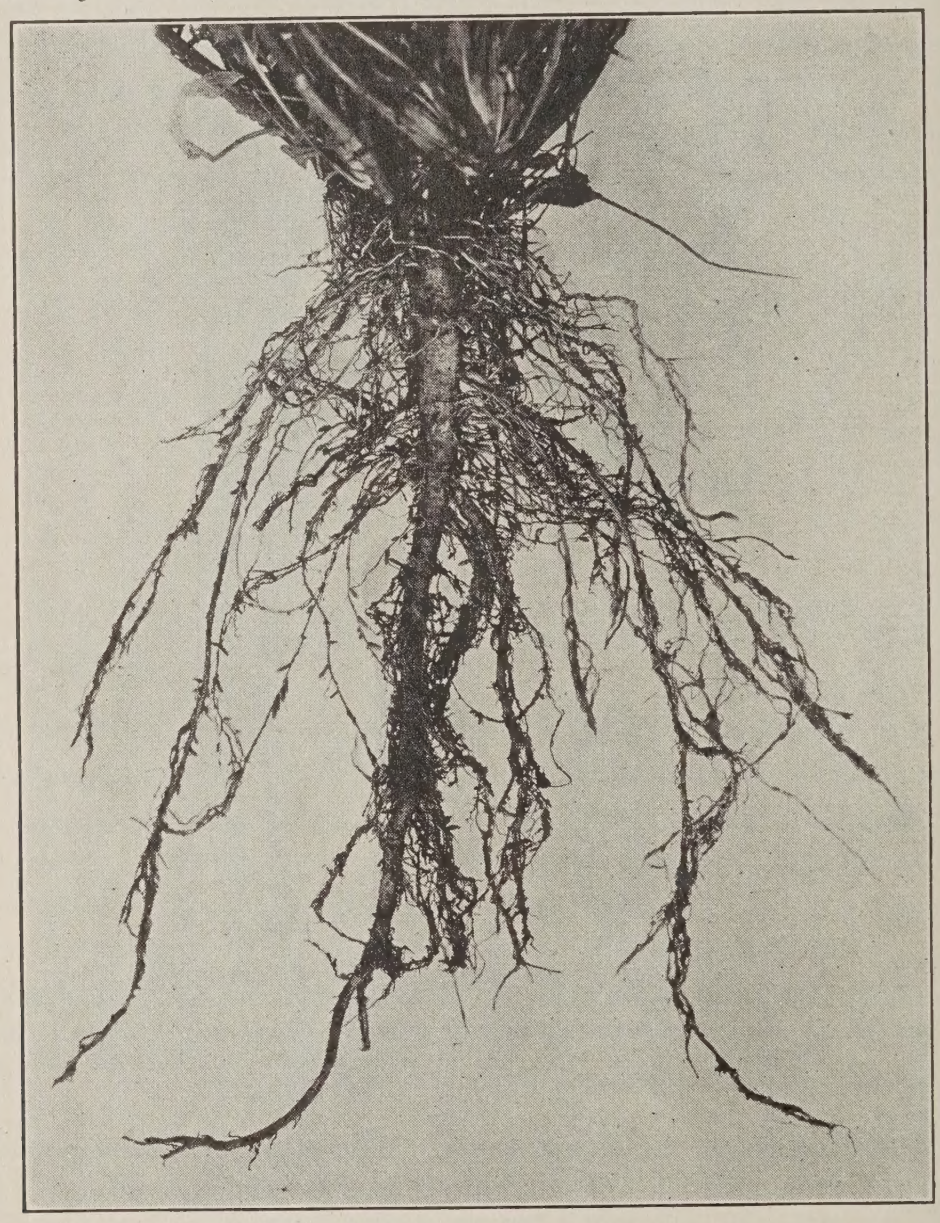


FIG. 7.—Root-system of a plant of red clover, showing tap-root and the fibrous rootlets. Much of the root-system (which may extend to a depth of 9 ft.) has been left in the soil.

Germination.—So long as the clover seed remains dry it continues to appear lifeless, and, indeed, if allowed to remain dry for too long a time it really becomes dead. But if it is planted in the soil, or in moist moss or sawdust, and kept at a suitable

temperature it soaks up moisture and swells; shortly the peg or embryonic stem (hypocotyl) begins to elongate and forces its way through the seed-coat. As growth continues the hypocotyl

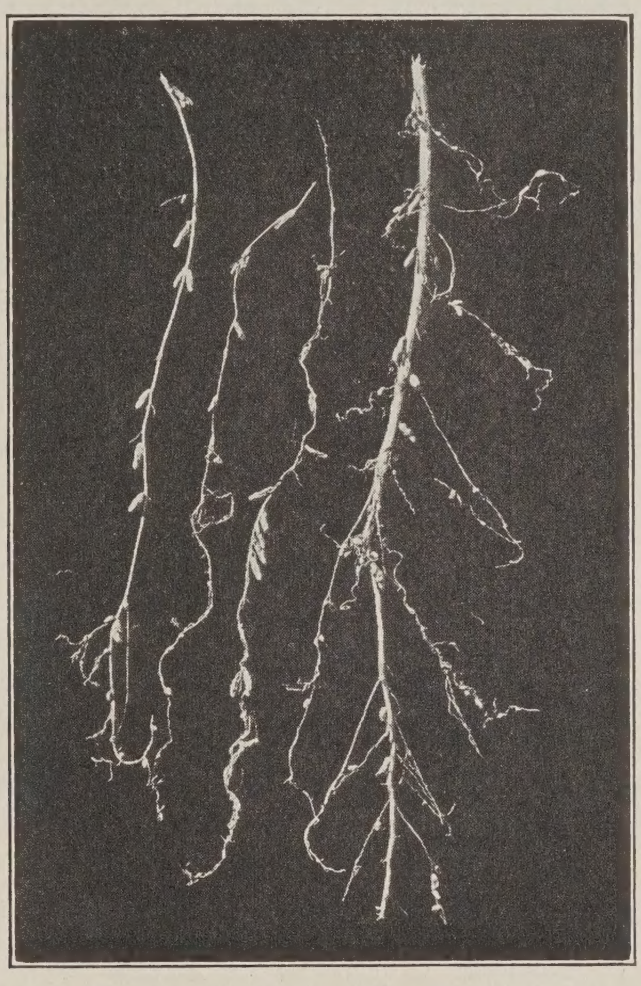


FIG. 8.—Rootlets of red clover showing the *root-tubercles*.

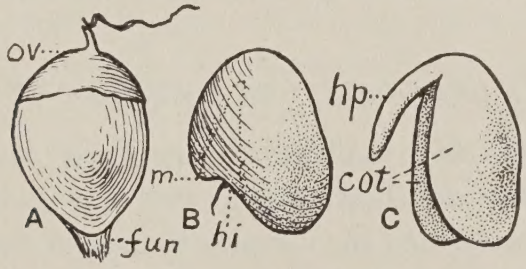
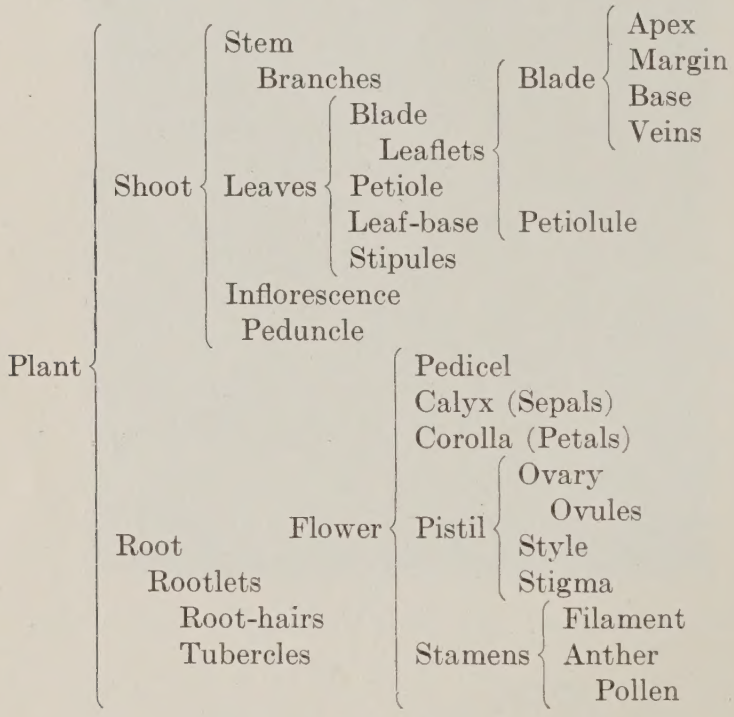


FIG. 9.—*A* and *B*, seeds, *C*, embryo of red clover. *ov*, remains of ovary-wall (with withered style) still adhering to the seed; *fun*, funiculus; *m*, micropyle; *hi*, hilum or scar; *hp*, hypocotyl; *cot*, cotyledons.

will curve (if necessary) so that the tip will penetrate downwards through the soil, and the stem become erect or vertical. Soon

the first or primary root begins to grow from the tip of the hypocotyl; the cotyledons, carried up into the sunlight and air, begin to enlarge and turn green, and the plumule begins to elongate and produce the second segment of the shoot. While these changes are going on above ground the roots begin to increase in number and length in the soil, root-tubercles begin to form, leaves and flowers develop on the stem, and eventually we have another plant like the one with which we started, thus completing the *life-cycle* of the plant.

The various parts of a clover plant mentioned in the preceding description, together with their subdivisions and their relation to each other, are shown at a glance below.



PROBLEMS SUGGESTED BY THE OBSERVED FACTS

We have briefly described the clover plant, and learned something of its parts and their names, but if this examination has not raised any questions in our mind—has not aroused our curiosity to know more about the plant, and to *explain* these facts and interpret their meaning, then we are not scientifically minded, for, as the great Swiss botanist, de Candolle, has said, "The interrogation point is the key to all the sciences." To the botanically minded the questions come thick and fast: What is the

stem for, why is it branched, why cylindrical? Why is the leaf-blade thin, flat, and green? Why is it compound, and why lighter green underneath? What is the use of the petiole, and of the stipules? What is the meaning and cause of the stipules? What is the meaning and cause of movements of the leaflets? Obviously the roots hold the plant in the soil, but do they serve any further purpose? What is the significance of the root-tubercles? What are the flowers for, and why are the older ones reflexed? What causes the deeper color at about the time a flower begins to turn down, and is it of any advantage to the plant to have the florets aggregated in a head? What is the relation of clover to other plants and to animals, and to the physical factors of its surroundings or *environment*, such as light, heat, and moisture? How are clover seeds made, and what causes growth? How did there come to be clover plants in the world; where are they native, and where introduced, and what is the significance of clover in our own daily lives? These and a multitude of other questions crowd upon us and demand answers; the answers, extended to all plants, constitute the great body of botanical knowledge. Many of these questions have never been satisfactorily answered, or have been answered only in part. Our ignorance is greater than our knowledge, and the gaps in our knowledge constitute one of the great incentives to botanical investigation or research.

Another great incentive to a study of plant life is the fact that a knowledge of plants is not only of great use, but is absolutely indispensable for the successful development and prosecution of certain occupations and industries, such, for example, as agriculture in all its branches. *The only way to learn about plants is to study plants*, and not to depend wholly upon books about plants, though books are helpful, and even essential as an aid to this study, especially in the beginning. He who hopes really to understand plants, however, must, as Agassiz said, get his facts from nature, fresh, buoyant, exact.

In the following chapters an endeavor will be made to answer some of the questions raised by a study of the clover, and to show how a knowledge of plant life is not only worth while for its own sake, and a source of personal satisfaction and pleasure, but is also fundamental to successful agriculture.

CHAPTER II

THE CELL

In the preceding chapter, we have briefly surveyed the parts (*external anatomy*) of a plant. But, just as a locomotive engineer needs to understand the construction of his engine so that he may know how it works and be able to run it successfully, so the agriculturist needs to understand the structure of plants in order to know how they "work," and to be able to control their behavior in the successful production of crops. A study of a plant with the unaided eye enables us to learn certain facts about its external features. We have seen, for example, that the clover plant is composed of certain parts or *organs*. In the economy of the plant each of these organs has one or more definite tasks to perform, known as its *function* or functions; but to understand how an organ performs its work we need to understand its inner structure. Just as the organism is composed of organs, so each organ is composed of *tissues*, and each tissue is made up of innumerable complex units of structure called *cells* (Figs. 10 and 11).

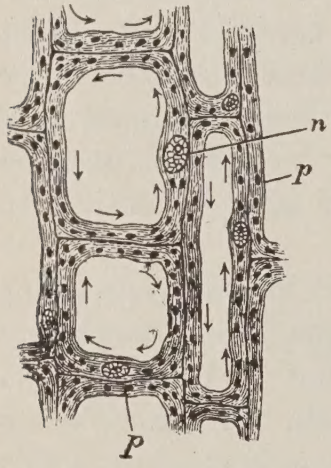


FIG. 10.—Cells from a leaf of Water-weed (*Elodea*). *p*, protoplasm in which are imbedded the nucleus (*n*), and numerous chloroplasts. The arrows show the direction of motion of the protoplasm. (After Reynolds Green.)

The elements of structure may be grouped as follows:

Organism
Organ
Tissue
Cell

The study of function is *physiology*, and all physiology is, in the last analysis, cell-physiology, for the physiological work of plants, as well as of animals, is performed by cells.

What is a Cell?—When the microscope was first invented men began to examine plant and animal tissues, and soon learned that these tissues had the appearance under the microscope of being made up of little compartments. Robert Hooke,[1] an Englishman (1635–1703), examined, among other objects, thin slices of bottle cork, and it was he who first called the structural units cells (1667), because of the resemblance of the tissue to a honey-comb with its compartments or "cells." The term was thus applied at first to the cavities, enclosed by the cell-wall, and the early studies were largely confined to the walls, or, in other words, to the skeletons of the tissues.

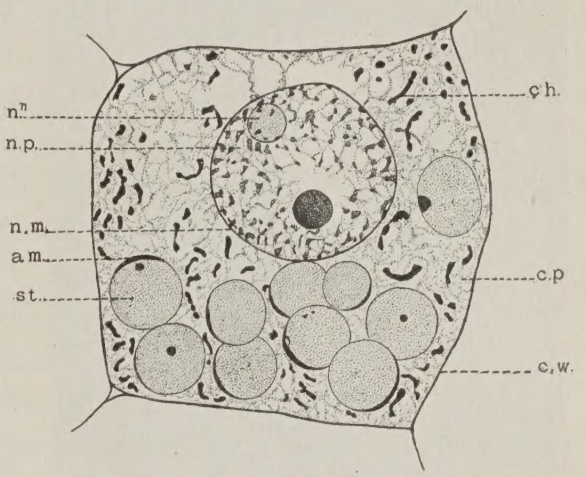


FIG. 11.—Cross-section of a cell from the root of a marrow-fat pea. n^n, nucleolus; *n. p*, nucleoplasm; *n.m*, nuclear membrane; *a.m*, starch-forming plastid; *st*, starch grain; *c.w*, cell-wall; *c.p.*, cytoplasm; *ch*, chondriosomes; they are scattered throughout the cytoplasm. (After D. M. Mottier.)

Protoplasm.—Soon after living tissue began to be studied it came to be recognized that the really important part is the substance enclosed by the cell-wall. Hugo Von Mohl[2] (1851), called this substance *protoplasm*, since it was understood to be the first substance formed by the plant, even before the cell-walls were made. In fact it was finally recognized that the cell-walls were made by the protoplasm. The term cell, therefore, gradually came to have a meaning quite different from that which it first had. As now defined *a cell is a unit of living matter or protoplasm*,

[1] ROBERT HOOKE. *b.* Isle of Wight, July 16, 1635; *d.* March 3, 1703. One of the founders (with Malpighi, Grew, and von Mohl) of plant anatomy. He greatly improved the compound microscope (1661), and (in 1665 or 1667) published, in London, his important book, *Micrographia or some physiological descriptions of minute bodies made by magnifying glasses.* He discovered the cellular structure of plants by examining charcoal, cork, pith, and other plant tissues under his microscope.

[2] HUGO VON MOHL. *b.* Stuttgart, April 8, 1805; *d.* Tübingen, April 1, 1872. One of the founders of plant anatomy. First to describe vegetable cell-division (1835); introduced the term *protoplasm* (1851). He was noted for the accuracy of his observations, drawings, and descriptions.

together with the cell-wall which surrounds it. It is not a cavity, but a substance (or substances). In recent years the term *protoplast* has come into general use to designate the unit mass of protoplasm within the cell-wall. Not all cells are enclosed by a cell-wall.

The Structure or Organization of a Cell.—Most plant cells are too small to be seen with the unaided eye, and their structure can be studied only with the aid of the compound microscope. If one of the young leaves of the Water-weed, *Elodea*, is mounted in water on a glass slide and examined under the microscope, the cells of which it is composed may be clearly seen (Fig. 10). The leaf-blade is only one cell or a few cells in thickness, and the most conspicuous objects within the cell-wall are the green *plastids* or *chloroplasts*. Commonly these bodies are in constant motion of *rotation*, passing up one side of the cell, thence across and down the other side. These chloroplasts are imbedded in the translucent, finely granular-appearing *protoplasm*, in contact with the inner surface of the cell-wall throughout. The circulation of the chloroplasts is due to currents in the protoplasm. Careful observation will reveal what appears to be a circular area of more dense protoplasm. This is the *nucleus* (Fig. 11). The cell-nucleus was first discovered and described by Robert Brown.[1]

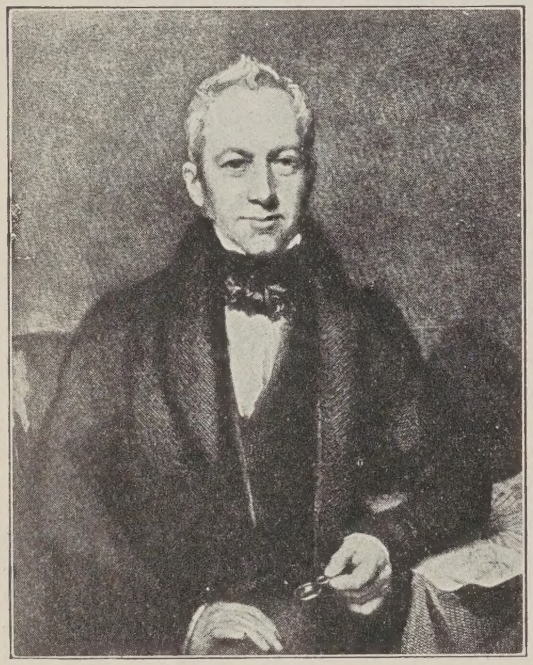


Fig. 12.—Robert Brown (1773–1858). One of the greatest of English botanists. He discovered the nucleus in cells, and also that Conifers and Cycads are gymnosperms.

[1] Robert Brown (1773–1858). Custodian of the British Museum (1823–1858). He was called by Humboldt "*Botanicorum facile princeps*" (easily the foremost of botanists). He not only made the first study of the cell-nucleus, but also discovered that conifers and cycads are gymnosperms, and was the first correctly to interpret the parts of the seed known as hilum, micropyle, and endosperm. He collected (in Australia) nearly 4000 species of plants new to science.

It is clearly distinguished, and is constantly changing its position owing to the motion of the protoplasm, and it will be seen that currents are passing in various directions along the strands of protoplasm, and that the pattern made by the strands is also continually changing. Since the nucleus is always imbedded in the cytoplasm it is commonly peripheral in older cells (Fig. 10).

The protoplasm may be seen to better advantage in a cell which has no chloroplasts, such, for example, as the cells of the tiny hairs on a squash seedling. When these hairs are mounted in water and examined with the microscope the protoplasm shows with great clearness, especially in the cells at or near the base of the hair. It is seen to occur as a layer against the inner surface of the cell-wall, and in strands of varying thickness extending across the cell-cavity, branching and uniting to form a sort of network.

Protoplasm belongs to the class of substances known as colloidal solutions or *sols*. When a crystal or crystalline substance (*crystalloid*), such as sugar or salt, is dissolved in a liquid a true solution results. When this occurs, all or most of the molecules of the dissolved substance may (in certain substances) become separated into component parts. The dissolved substance will diffuse through a semi-permeable membrane, as described later, in Chapter III. When a solution evaporates, the liquid passes off in the form of vapor, and the particles of the dissolved substance again come together and form crystals identical in form and structure with those originally dissolved.

There is another class of substances, however, such as proteins, gums, gelatine, agar, and others, which may become evenly distributed throughout the mass of a liquid in a manner resembling the solution of a crystal, but such substances will not diffuse through a membrane, and when the liquid evaporates the finely divided particles of the solid do not form crystals. Such substances are called *colloids*.

Some crystalloids may be made colloidal and are then said to be in the "colloidal state." In fact most metals and even such typical crystalline substances as common table salt may occur in the colloidal state—a state of dispersion in a liquid of particles which may be either very large molecules or aggregates of mole-

cules. They are too small to be seen with the highest powers of the microscope.

Many colloidal substances (*e.g.*, agar and gelatine) are in the liquid state only at certain temperatures, and when the colloidal solution cools they "set" to form *gels*. This process underlies the making of "jelly" out of the various fruit juices which contain a carbohydrate substance called *pectin*. This occurs chiefly in the juice of comparatively acid fruits such as currants, apples, grapes, and others; it occurs only slightly, if at all in other types of fruit, such as bananas, pears, and oranges. When the fruit juice is boiled the pectin passes into colloidal solution, and when the solution cools it solidifies into a gel, forming "jelly."

Protoplasm may be regarded as a complex and unstable colloidal mass—a *polyphase colloidal system*, comprising water with various substances in solution, emulsion, and colloidal suspension. This enormously facilitates chemical reactions in the protoplasm, but whether or not all "living" phenomena may be explained on this basis, we have not yet sufficient knowledge to say.[1]

The spaces within a cell not occupied by protoplasm are filled with a watery solution of various substances (salts, sugars, etc.) which also saturates the protoplasm itself. This is the *cell-sap*, and the spaces filled with the cell-sap, but not occupied by protoplasm, are called *vacuoles*. The term *cytoplasm* is now commonly used to distinguish the cell-plasm from the nucleus.

Vacuoles.—In very young (embryonic) cells the space within the cell-wall is more nearly completely occupied by the protoplasm than in older cells, and the vacuoles are smaller and appear as minute droplets of liquid distributed through the mass of the cell. In cells of this age, also, the nucleus commonly occupies a position at or near the center of the cell. In older cells the vacuoles are larger, and the cytoplasm occurs in thick strands, as described above. In mature or old cells the protoplasm is largely, or wholly confined to the periphery, forming, as it were, a sac, the *primordial utricle*, of older writers, in close contact at all points with the cell-wall, and enclosing one large vacuole full of cell-sap.

[1] Such phenomena as the coagulation of blood, the formation of blood clots, and the stiffening of dead animal bodies (*rigor mortis*) are caused by the change of the colloidal solutions in the blood and in muscle cells to gels.

Pulsating or *contractile vacuoles* are of general occurrence in cells of the lower animals (*Protozoa*), such as *Amoeba*, *Paramecium*, and others, and have long been recognized in the so called "swarm spores" (motile reproductive cells) of certain Algae. Recently contractile vacuoles have been described by Lloyd[1] as normal organs in the conjugating cells of the green alga, *Spirogyra*, and their action has been demonstrated by Lloyd by means of motion pictures, photographed through the compound microscope. These vacuoles appear and disappear in rhythmic pulsation owing to the contraction of the walls of the vacuoles. Their function in protozoa is believed to be that of excretion. In *Spirogyra* one of their functions is to assist in the passage of one protoplast into the cell-cavity of another protoplast in the reproductive process of *conjugation*, to be described later (p. 457).

Plasma Membrane.—The free surfaces of all liquids behave like a membrane, often called the *limiting membrane*. This is clearly illustrated in the simple experiment of causing a sewing needle to float on water in a glass merely by placing it horizontally on the surface with sufficient care not to puncture the surface membrane. All free surfaces of protoplasm behave like a membrane. This *plasma membrane* forms the walls of the vacuoles. The surface of the nucleus is the *nuclear membrane;* the surface of the entire protoplast is the *limiting membrane*[2] of the cell.

Nucleus.—In order to study the parts of the nucleus it is usually necessary to use tissue that has been specially prepared by killing it quickly so that the protoplast does not shrink. Extremely thin slices or sections are then cut, and stained so as to render the parts more easily visible. Figure 11 is reproduced from a drawing made of a cell from tissue of a pea root, prepared as just described. The large, conspicuous circular body is the nucleus. It is globular in form, and thus appears circular in section. The nuclear membrane is clearly shown, enclosing the *nucleoplasm* (as distinguished from the cytoplasm). The nucleo-

[1] Lloyd, Francis E. Conjugation in Spirogyra. Trans. Royal Canadian Inst. **15**: 129–134. 1924.

[2] Whether there is an actual membrane or not at the free surfaces of protoplasm has been questioned, and some investigators have used the noncommittal term, *limiting surface*, instead of limiting membrane.

plasm, at the stage here shown, forms a network, and the portion that deeply stains, is, on that account, called *chromatin*. The chromatin is distributed on a network of delicate threads called *linin*. The nucleus usually contains one or more "little nuclei" or nucleoli (sing. *nucleolus*), and the space not occupied by structures contains *nuclear sap*.

Outside the nucleus, in figure 11, are shown the circular sections of numerous globular starch grains, each formed by the *plastid* shown at one side. Scattered through the cytoplasm are many small bodies, staining deeply like the chromatin, and called *chondriosomes*, or *mitochondria*. Their function or significance is not clearly understood. The parts of a cell may be shown diagrammatically as follows:

- Cell
  - Cell-wall
  - Protoplasm
    - Cytoplasm
      - Limiting membrane
      - Vacuoles
      - Vacuolar membranes
      - Cell-sap
      - Plastids
      - Chondriosomes
      - Other contents (inclusions)
    - Nucleus (nucleoplasm)
      - Nuclear membrane
      - Chromatin
      - Linin
      - Nuclear sap
      - Nucleolus

Properties of Protoplasm. *a. Metabolism.*—Thus far we have only considered the appearance of protoplasm, and its structure. But the most significant thing about it is its behavior. The cell has been fittingly compared to a factory where raw materials are being received, transformed into manufactured products, and sent out to places where they are needed. In this process there result various waste and by-products, and the delicate machinery is constantly being worn out and is thus in need of constant repair. That which chiefly distinguishes protoplasm from every other known substance is its ability to rebuild itself—to transform other and non-living substances into living protoplasm. It is constantly wasting away, and constantly rebuilding itself—under-

going incessant destruction and continuous reconstruction. The sum total of these transformations is called *metabolism;* when the processes of construction exceed those of destruction the cell increases in size and substance; when the reverse occurs the protoplasm gradually wastes away and the final result is death. Constructive metabolism is called *anabolism*, and the reverse process is *katabolism.* A more common term for anabolism is *nutrition.*

b. Reproduction.—Not only does a healthy plant maintain itself by nutrition, but every plant is so organized that it can reproduce other individuals like itself. In other words, the production of seeds (or its equivalent) is the natural culmination of the life of every healthy plant. This function of reproduction is manifested by every embryonic or undifferentiated cell, which sooner or later reaches a stage where it can preserve its own life only by sacrificing its individuality and dividing into new cells—the so-called "daughter-cells."

c. Irritability.—Protoplasm is very sensitive. We are familiar with the evidence of this in the case of our own nerves, but "nervous" irritability is not confined to animals, nor even to nerve tissue; it is a property of all protoplasm, plant or animal. Because of this property, protoplasm is able to detect changes in its environment, such as alterations of light, temperature, moisture, the pull of gravity, contact, and chemical change, and to react to those changes. Any change in the environment may become a *stimulus* to the protoplasm, and the reaction is termed the *response to stimulus*, or simply the *reaction.* Living things are dependent upon this property for their very existence, for every organism must be in harmony with its surroundings in order to keep healthy and to function normally. As a plant grows it becomes adjusted to certain conditions of environment, and if any of these conditions is altered in any way, a readjustment is necessary on the part of the plant. It is obvious that such a readjustment could not occur unless the plant were sensitive to the changes. Abundant illustrations of this will be found in the following pages, and many will no doubt occur at once to the reader.

Chemistry of Protoplasm.—If the preceding paragraphs have been understood, it will be understood that protoplasm is not a

chemical substance like salt, or sugar, but a mechanism, comprising the different organs of the cell. Of the various parts—cytoplasm, nucleoplasm, cell-sap, plastids, and other inclusions, each has a physico-chemical composition different from the others. Protoplasm, therefore, cannot be expressed by a chemical formula. Further discussion of the chemistry of protoplasm must be reserved for more advanced courses.

Nuclear and Cell Division.—When cells divide to form new cells, the nucleus divides first by a complex process of marvellous delicacy and precision. In the non-dividing nucleus (sometimes

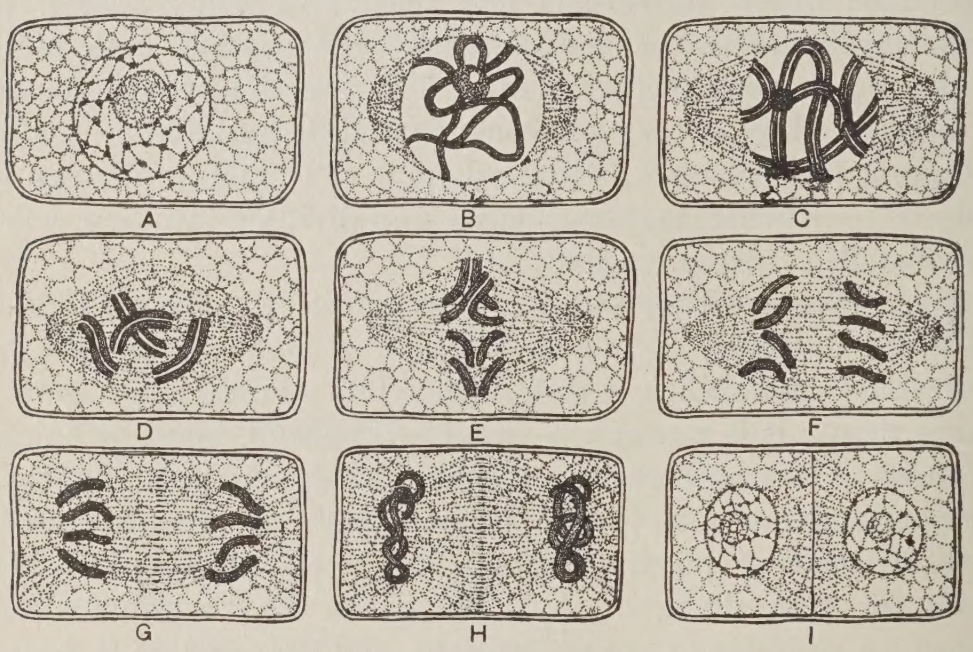


FIG. 13.—Diagram illustrating various stages of indirect nuclear division (mitosis). *A*, resting nucleus of the mother-cell; *B*, formation of nuclear skein or spirem; *C*, longitudinal splitting of the spirem; *D*, the chromosomes (four in number) have been formed by the transverse segmentation of the spirem; *E*, chromosomes arranged on the equator of the nuclear spindle; *F* and *G*, early and late *anaphase*, the chromosomes moving to the poles of the spindle; *H*, formation of daughter spirems; *I*, resting stage of the two daughter cells.

called the resting nucleus) the chromatin, as noted above, is distributed on the linin threads in the form of minute granules (Fig. 13). At one of the stages preliminary to nuclear division the linin network, with the chromatin, becomes transformed into a thick *skein*, which shortly becomes split into two throughout its entire length. The skein finally becomes divided transversely into a number of double chromatin bodies or *chromosomes*. The number of these chromosomes is characteristic and always the

same (in the body-cells) for each species of plant or animal (see p. 972).

After the formation of the chromosomes the nuclear membrane disappears, and, by a complicated mechanism, not entirely understood, the two halves of the chromosomes are separated and carried apart to opposite sides of the cell. After this division of the nucleus a new cell-wall forms, dividing the entire cell into halves; new membranes develop, and the chromosomes in each *daughter-nucleus* become gradually transformed into a resting nucleus.[1]

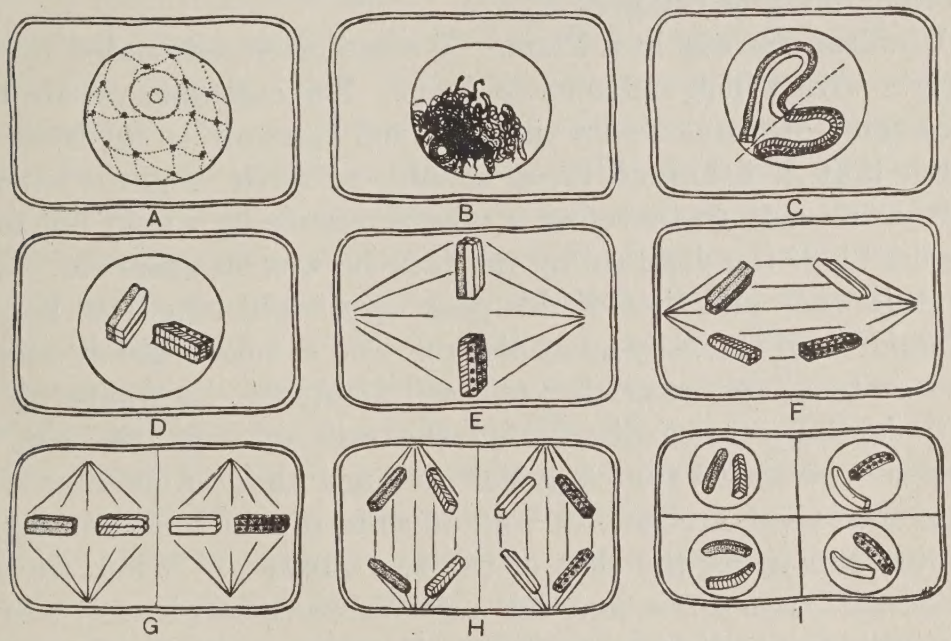


FIG. 14.—Diagram illustrating various stages in the reduction division (maiosis) of a spore-mother-cell of a plant. *A*, resting stage of the mother-cell-nucleus; *B*, the nuclear skein or spirem, in synizesis (during synapsis); *C*, the spirem after synapsis, showing its double (diploid) nature; the dotted line indicates the segmentation of the spirem into two diploid chromosomes, each of which has split longitudinally in *D*; *E*, the diploid chromosomes on the equator of the spindle of the first (heterotypic) division; *F*, late anaphase; *G*, metaphase of the second or homotypic division; *H*, late anaphase of same, two haploid chromosomes approaching the poles of each spindle; *I*, the four daugher-cells (spores) of the tetrad.

Reduction Division.—In the formation of reproductive cells (*e.g.*, *spores*, *egg-cells*, *sperms*) a new resting nucleus is not organized after the first nuclear division by which the number of

[1] The term "resting" nucleus means merely that the nucleus is not dividing. Physiologically speaking, it is not resting; nutrition, respiration, and other processes may be and doubtless usually are more or less active.

chromosomes in each nucleus is *reduced* by one-half, but this division is followed at once by a second. This is the process of *tetrad-division*, by which four spores are formed from each *spore-mother-cell*. The reduced or *haploid* number of chromosomes then persists up to and including the formation of egg-cells and sperms. When a sperm and an egg unite, in reproduction, the nucleus of the resulting reproductive cell will, of course, possess the original or doubled (*diploid*) number of chromosomes, which now persists until spore-formation again takes place. The steps in reduction are illustrated in Fig. 14. This subject is treated more in detail in Chapter XLI.

Number of Cells in a Plant.—We are often astounded by the figures with which Astronomy deals. For example, we are told that some of the not very distant fixed stars are so far from the earth that, if a human being should, at birth, begin a journey thither on a train traveling a mile a minute he would not have covered half the distance by the time he was 90 years old. The botanist may add that, if this passenger could take with him an average sized tree, say an apple tree, and should begin at once to pick it to pieces, removing one cell a minute, he would by his 90th birthday have distributed the cells of only one leaf, for Bessey[1] calculated that in a leaf no larger than an average sized apple leaf there are fully 50 million cells, of which no less than 8 million constitute the skin of the two surfaces. When we now recall that such a tree may have several thousand leaves, besides the cellular tissue of roots, trunk, branches, and other parts, we see at once that the mind cannot comprehend a number sufficiently large to designate how many cells there are in the entire tree.

Historical Influences.—We can never understand nor interpret a given protoplast, nor the organism of which it is a part, unless we know something of its past history. It is often difficult if not impossible to tell, by looking at a given cell, from what kind of a plant it has come; so sometimes it is even difficult to say whether the cell is from an animal or a plant. Chemical analysis may even reveal the same chemical elements and compounds in the protoplasm of different plants, and the structure or organization of a cell is one of the most conservative features of plant or animal

[1] Bessey, C. E. The botany of the apple tree. Ann. Rept. Nebraska State Hort. Soc. 1894, p. 17.

life. There are, to be sure, cells of simple plants, like the bacteria, where no nucleus has yet been detected, or where the nuclear substance is diffused through the protoplasm rather than organized into a definite nucleus, but, for the most part, the evolution of plants has not involved any fundamental change in the organization of the plant cell. That is, from the lower plants to the highest, the differentiation into cytoplasm, vacuoles, plastids, nucleus, and even the finer parts of the cell, as given in the table on page 20, is everywhere present, and in their general nature and functions, and in their relations to each other, these structures are essentially the same. It is one of the great outstanding facts of evolution, says Harper,[1] that "it has not consisted in the production of new types of protoplasmic structure or cellular organization, but in the development of constantly greater specialization and division of labor between larger and larger groups of cells"—that is between tissues, organs, and organisms. The differences between various kinds of plants and animals may not, therefore, be explained by differences in their structural or morphological organization, as outlined above. But all protoplasm possesses something which cannot be detected by the most careful observer with the most powerful microscope, nor revealed by the chemist with the most refined methods of analysis; it is only revealed in the processes of growth, development, and reproduction. It is in virtue of this that wheat plants, for example, are always produced by wheat seed. As we shall learn in a subsequent chapter, careful investigation has led to the conclusion that this "something" occurs chiefly, though possibly not exclusively, in the chromatin of the cell, and that it occurs in the form of units called *genes* (from a Greek word meaning "to become," or "to generate"). As to the nature of the genes—whether they are molecules, tiny groups of molecules, or merely a definite relationship existing between particles of matter—no one knows. In the division of cells they behave with mathematical precision, as we shall also see later on, and they are believed to hold the key to the phenomena of inheritance.

This is why the past history of the protoplasm in a plant or animal is of such importance, for that determines, in part, what

[1] Harper, R. A. The structure of protoplasm. Am. Jour. Bot. 6: 277. 1919.

genes shall enter into its chromosomes, which is only another way of saying "what its inheritance shall be." A phonograph, like a cell, is a mechanism, but it functions without particular reference to its past—where the materials of which it is made were obtained, or who was the workman or maker. It is a new creation without any past *as a phonograph,* and will reproduce a record of any make. The record itself, on the disc, has a closer analogy to the living cell, for it has, in a sense, had a history as a record; it has had impressed upon it by another (original) record, (its "ancestor") through the medium of sound waves (part of its environment), certain characteristics which distinguish it from all other records except those of the same history (ancestry and environment); placed in the phonograph it will always reproduce the tune it has "inherited," so to speak, and no other.[1] The analogy is, no doubt, crude and loose, but perhaps not misleading. The point we are emphasizing is that the behavior of a certain mass of protoplasm, and therefore of the organism produced by this protoplasm, depends, not only upon its visible structure, its chemical composition, and its environment, but also, and in largest measure, upon its past history as protoplasm or plant—upon its inheritance, the genes it received from its ancestors. This is one of the most fundamental of all the properties of living things.

But, however much plants may differ in structure and heredity, they are all alike in the fact that they must be supplied with water and nutrients from without. In the next chapter we shall consider the problem of the absorption of water and mineral nutrients.

[1] The analogy may even be extended, if desired to include a "Creator" of the original ancestor of this line of records—the singer whose voice produced the first record from which the others were made.

PART II

THE VEGETATIVE FUNCTIONS OF PLANTS

CHAPTER III

THE ABSORPTION OF WATER AND MINERAL NUTRIENTS

"No water, no crops, no animals, no human life—indeed no soil." In these words a recent writer has tersely stated the dependence of agriculture on an adequate supply of water. The fundamental need of plants becomes the fundamental need of the basic human occupation, and therefore of human life, industry, civilization. In studying the water relations of plants it will be convenient to consider, in order, the percentage of water in plant tissue, the water requirements of plants, the organs of absorption, and the physical processes by which absorption takes place.

Rough Analysis of Plant Substances.—We have learned that a plant is composed of organs, the organs of tissues, the tissues of cells, which are composed of protoplasm surrounded by cell-walls, and finally that protoplasm, while not a chemical substance itself, is made up of substances each of which has its own peculiar physical characteristics and chemical composition. We may gain a further insight into the composition of plants if we make a rough analysis of plant substance. A potato tuber will serve as well as anything. The tuber should first be washed to remove any soil that might be adhering, and the surface thoroughly dried. We have at hand an accurate balance for weighing, and ascertain and record the weight of the tuber. We then cut the tuber across into four or five pieces and dry these pieces thoroughly in a drying oven at a temperature of about 100° F., until, on successive weighings, they are found not to lose weight. By this process we have driven off all the water and have left only the dry substance of the tuber.[1] This is carefully weighed

[1] A small portion of the dry substance is of course lost in the process of cutting the tuber into pieces, but the amount is so slight as to be negligible for the purpose we have in hand. The tuber is weighed before cutting to avoid loss of water by evaporation from the cut surfaces.

and the weight subtracted from that of the tuber before dessicating. The difference in the two weights is the weight of the water, driven off as water-vapor. By this analysis we learn that substantially three fourths, or 75%, of the weight of the tuber is due to water, and only one fourth to dry matter. A large excess of water over dry matter is true of the fresh tissue of nearly all living things, whether plant or animal. Moreover, we do not need to study botany to know that plants are constantly losing water; house plants must be continually watered, garden vegetables wilt in the market, crops wither and fail in drought. The great, and primary, need of plants, therefore, is water.

Water Requirements of Plants.—Analyses have been made of nearly all farm crops, and the following figures may be taken as illustrating in general the relative amounts of water and dry substance in crop plants.

TABLE I.—PERCENTAGE OF WATER IN CROP PLANTS

Material	Percentages of	
	Dry subst.	Water
Clover plant	22.0	78.0
Potato tuber	25.0	75.0
Wheat grain	85.7	14.3
Wheat flour	87.3	12.6
Bean seeds	85.0	15.0
Oat grains	85.7	14.3
Meadow grass (fresh)	20.0	80.0
Dry hay	85.7	14.3

But the amount of water to be found in plant tissue is not a measure of the amount required by the plant during its growth, for careful experiments with a large number of plants have shown that, on an average, some 310 pounds of water pass through and evaporate from a plant for every pound of dry matter formed. Since about 85.7% of hay is dry substance, two tons, of 2000 pounds each, contain about 3428 pounds. Allowing approximately two tons of hay to the acre, it may be calculated that one acre of meadow grass would evaporate 531 tons[1] of

[1] $\frac{(3428 \times 310)}{2000} = 531$

water during the growing season. Wheat yields on the average 720 lbs. of grain and 1500 lbs. of straw per acre. On the basis of the figures in the above table we may calculate that 265 tons[1] of water are given off by an acre of wheat during a season. About 100 tons of water fall on an acre of ground for every inch of rainfall; therefore a crop of hay gives off, per acre, the equivalent of about 5¼ inches of rainfall, and an acre of wheat about 2¾ inches. The remainder of the rain water soaks into the ground, or runs off in surface and sub-surface drainage, or evaporates into the air, or remains behind in the growing plants.

The amount of water that must be supplied to a plant in order to make possible the production of a given weight of dry matter is its *water requirement.*

The water requirements of eleven crop plants and three common weeds are given as follows by Briggs and Shantz. The figures in the last column of the table indicate the ratio

TABLE II.—WATER REQUIREMENTS OF PLANTS

Common name	Botanical name	Average water requirement
Crop plants		
Western wheat grass	*Agropyron Smithii*	1076
Flax	*Linum usitatissimum*	905
Alfalfa	*Medicago Sp.*	831
Clover	*Trifolium Sp.*	797
Rice	*Oryza sativa*	710
Potato	*Solanum tuberosum*	636
Oats	*Avena sativa*	597
Buckwheat	*Fagopyrum esculentum*	578
Barley	*Hordeum Sp.*	534
Wheat	*Triticum Sp.*	513
Corn	*Zea Mays*	368
Weeds		
Ragweed	*Ambrosia artemisifolia*	948
Purslane (Pussley)	*Portulaca oleracea*	292
Pigweed	*Amaranthus retroflexus*	287

[1] $\frac{(2000 \times 857 \times 310)}{2000} = 265$

These figures are, of course, only illustrative; they would vary widely with location, soil, weather, and especially with the variety concerned.

of the weight of water absorbed by a plant during its growth to the weight of dry matter produced, exclusive of the roots. The figures given are, in each case, the average of several determinations.

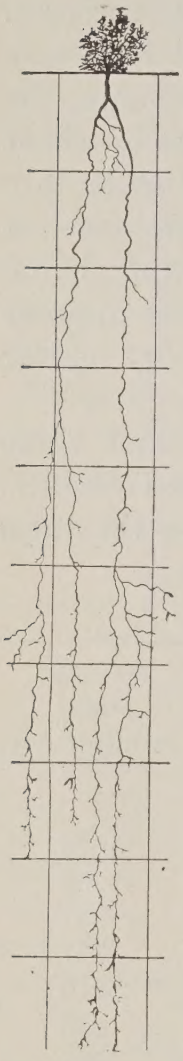


FIG. 15.—Root system of *Lithospermum linearifolium*, penetrating to more than 10 ft., in deeply moistened soil. Each square represents one foot. The upper horizontal line represents the surface of the soil. (After Weaver.)

"The Duty of Water."—The expression "duty of water" was first used by Powell[1] to indicate "the amount of water which is needed to serve an acre of land," measurable in acre-feet. Now, as McGee points out,[2] the average of all crops in food farming is six tons per acre a year, or approximately $\frac{1}{1000}$ of the weight of the water supplied by the soil each year to the roots of the growing plants. Thus, McGee defines the *agricultural duty of water* as the production of one one-thousandth part of its weight in average plant crop. On the basis of these figures it has been calculated that it requires two tons of water to produce one pound of bread; or on the basis of the average annual consumption of meat and bread by one adult human being, that "*the final duty of water* is to sustain a human life a year for each five acre-feet used effectively in agriculture." To be moderately productive, soil must deliver to crop-plants not less than 1.5 acre-feet of water each growing season.

Organs of Absorption.—It is a matter of common knowledge that plants absorb most of their water by their roots. When plants are watered, either by rain or artificially by sprinkling or irrigation, the water is applied, not to the foliage, but to the soil where the roots grow. It is also interesting in this connection to recall that when seeds germinate the first organ to develop from the embryo is a root, and not until the root is fairly well established in the moist soil do the stem and leaves of the

[1] Powell, W. J. The irrigable lands of the arid region. *Century Mag.* **39**: 770–771. 1890. An *acre-foot* is the amount of water required to cover an acre to a depth of one foot.

[2] McGee, W. J. The agricultural duty of water. *Year Book U. S. Dept. Agric.* **1910**: 167–176. 1911.

seedling appear above the surface. In fact, seeds will not begin to germinate at all unless supplied with a suitable amount of moisture. Experiments by Livingston showed that seeds of wheat will not germinate in soil containing less than 15%–20% of water by volume; radish seed required 20% or more, and red clover seeds 25% or more. In order to understand the process of absorption, we must learn something of the structure of roots.

Extent of the Root System.—The mere extent of the root system is significant here. In one experiment a plant of barley was grown in rich soil in a small box measuring between three and four inches in each dimension. When the plant was mature its root system was found to have a total length of 128 feet, (not including the root-hairs to be mentioned later). When growing freely in a field the root system may attain even greater lengths. The roots of an oat plant extending through less than two cubic yards of soil were found on careful measuring to have a total length of over 450 feet. Such root systems as these not only illustrate the extent of the absorbing surface of plants, but also indicate the importance of the roots in anchoring the plant firmly in the soil. Some plants, such for example as onions, are held very loosely in the soil, while others, like the potato, are anchored more firmly. A weed like the burdock can hardly be pulled up without leaving a large portion of the roots, especially the finer root-fibers, in the soil. Trees are so firmly anchored that they are able to withstand all ordinary and even severe winds.

The most thorough studies ever made of root systems are those of Weaver,[1] who investigated the root systems of 1500 native plants of our American prairies, plains, sandhills, forests, and chaparral. These studies were made for the purpose of acquiring knowledge that could be applied in crop-production, for, as Weaver states, a knowledge of root position of native plants, especially when interpreted in their community relations, so clearly reflects the moisture conditions of the soil that it aids not only in selecting the kind of crop to be most profitably grown, but also helps in

[1] Weaver, John E. The ecological relations of roots. Carnegie Institution of Washington. Pub. 286, Washington, D. C., Sept. 5, 1919.

Ibid. Root development in the grassland formation. Carnegie Inst. Wash., Pub. 286, 1920.

Ibid. Development and activities of roots of crop plants. Carnegie Inst. Wash., Pub. 316, May, 1922. Also other papers.

determining the most proper methods of tillage. The same investigator has also studied the root systems of cereal grains and other crop plants.

The method used involved the digging of a trench from 5 to 9 feet or more deep, 6 to 10 feet long, and of sufficient width to work in, by the side of the plant to be examined. Then by carefully removing the soil on the side of the trench next the plant the entire root system could be uncovered, drawn, and studied.

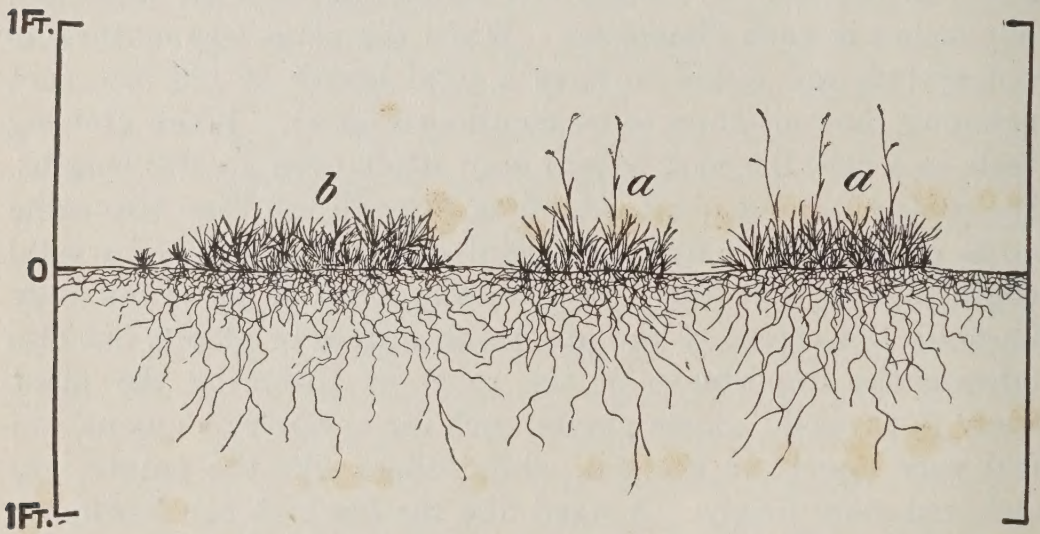


FIG. 16.—Sketch showing root systems limited to the surface soil where the moisture penetrates for only about 1 ft. *a*, Grama grass; *b*, Buffalo grass. (After Weaver.)

Additional care was necessary in excavating the deeper root systems. As might be anticipated, the characters of the root system are carefully correlated with the moisture conditions of the soil. If the moisture penetrates deeply into the soil, as on the prairies, so also do the roots (Fig. 15); if the moisture is largely confined to the surface layers, lateral roots develop in profusion near the surface (Fig. 16).

The extent of root systems is truly wonderful, and a revelation to one who has never given any special thought to the subject. In several cases, as, for example, *Rosa arkansana* and *Lygodesmia juncea*, the roots were traced to a depth of 18 or 20 feet or more. The most extensive root system described by Weaver is that of the bush morning-glory (*Ipomoea leptophylla*) a common plant in the sandhills. The plant appears to be a vine below ground as

well as above, the roots occupying a block of soil over 10 feet deep and 50 feet in diameter. "Indeed," says Weaver, "the surface foot of soil as well as the 10 feet below it were literally filled with the glistening white, brittle branches of this remarkable root system." The shoot system of the plant measured 7 feet in diameter and 30 inches high.

Plants growing on the sloping surface of a "gravel-slide" were found to send a tap-root with branches vertically downward to a depth of 30 inches, more or less, depending on the species, and to

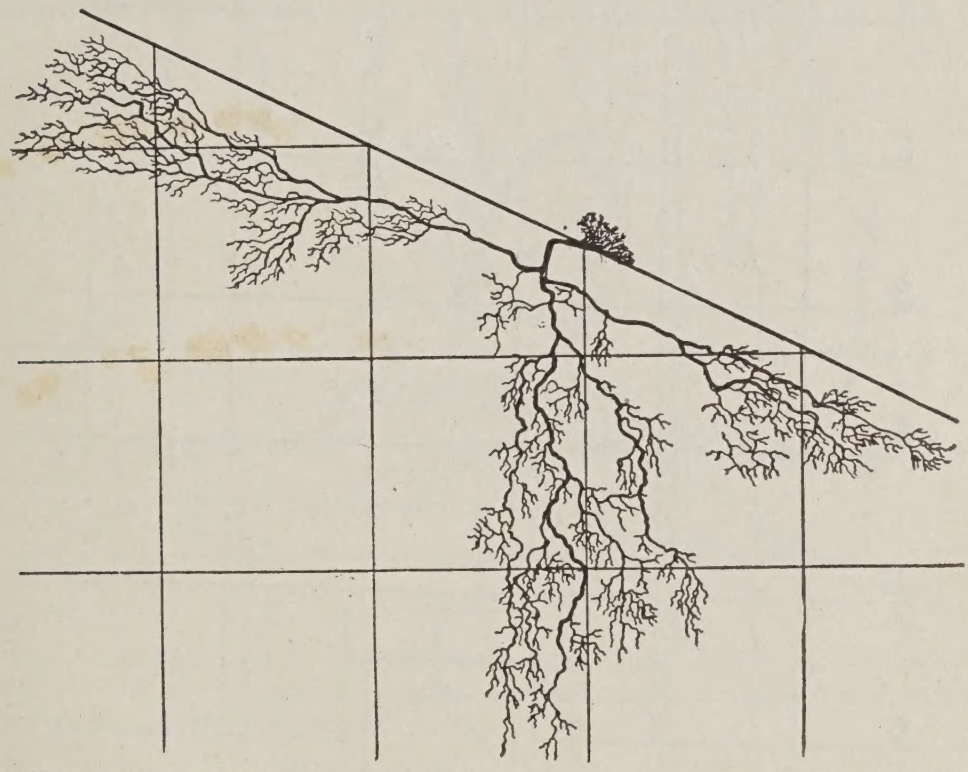


FIG. 17.—Root system of *Paronychia jamesii*, growing on the surface of a gravel slide. (After Weaver.)

send out lateral branches parallel with the surface, and extending both up and down the slope at a depth of about 2 to 4 inches (Fig. 17).

The application of a knowledge of the root systems of the native vegetation in helping to determine what character of cultivated plant is most likely to succeed as an agricultural crop in a given region is obvious, especially when supplemented by a knowledge of the root systems of crop plants.

In his 1922 memoir Weaver gives the results of his studies of the root systems of various cereals, of potato, and other crops.

Among other things, it was found that the primary roots of wheat (and other cereal grains), that spring from the hypocotyl during the germination of the seed, do not die before the plant is full grown, as some authors have contended; they continue to be the main roots during the entire life of the plant, being supplemented

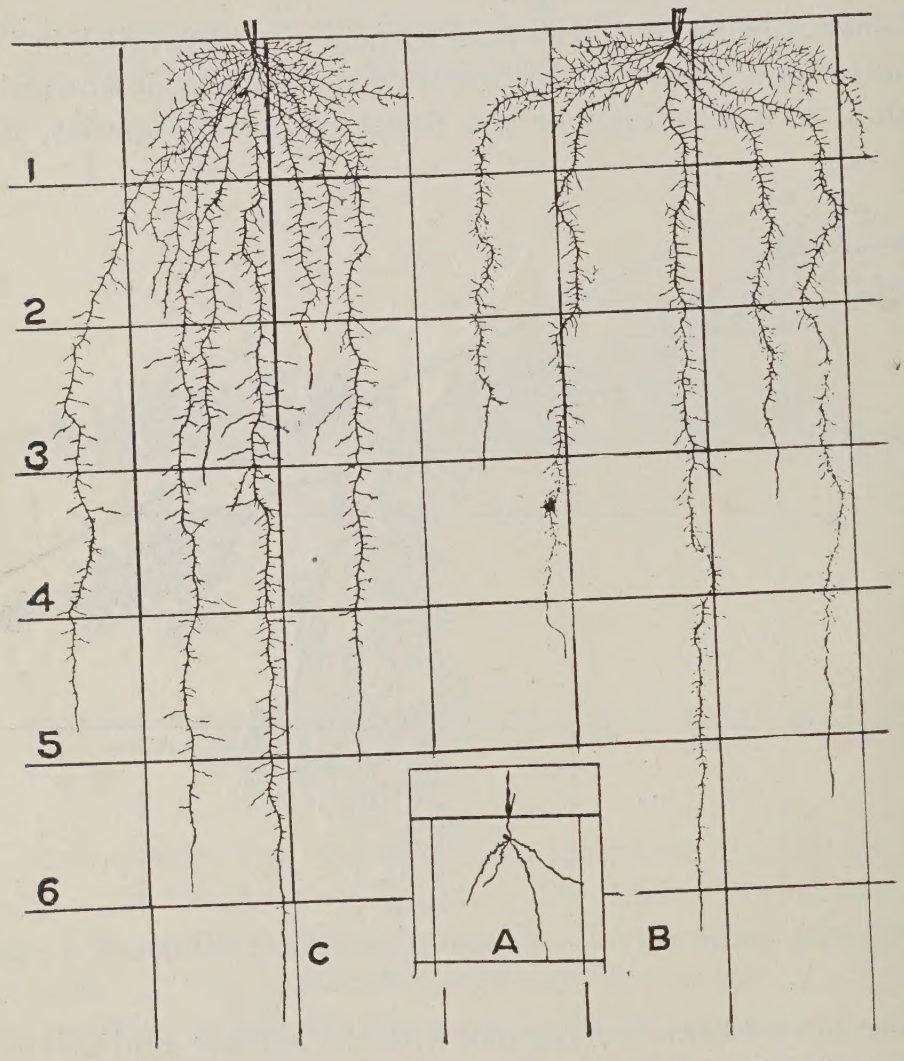


FIG. 18.—Showing persistence of primary roots of wheat after the secondary root-system has developed. *A*, Marquis wheat 20 days old; *B*, Marquis wheat at maturity; *C*, Durum wheat at maturity. In B and C in the upper half-foot of soil may be seen the remains of the seed-grain from which the deep-growing primary root-system grows. The roots that originate nearer the soil surface are the secondary roots of later origin. (After Weaver.)

by the secondary root system that forms later nearer the surface of the soil, thus giving substantially two root systems—a "surface-feeding" and a deeper absorbing system (Fig. 18). In one study Weaver found, in the case of mature Marquis wheat, 93 days

after planting, that plants 2.5–2.8 feet high, averaging 2 stalks each, had roots that penetrated to a maximum depth of 6.7 feet, being frequent at a depth of 5 feet; the soil was well filled with roots at a depth of 3.7–4.2 feet. The number and extent of the longer roots and their great depth of penetration is, as Weaver states, impressive, especially when compared with the height of the tops. This comparison is illustrated in figure 18.

The root-system of corn 36 days old and 116 days old (September 2), illustrated in figures 19 and 20, shows "a remarkably extensive and efficient" root system. Here also (Fig. 19) will

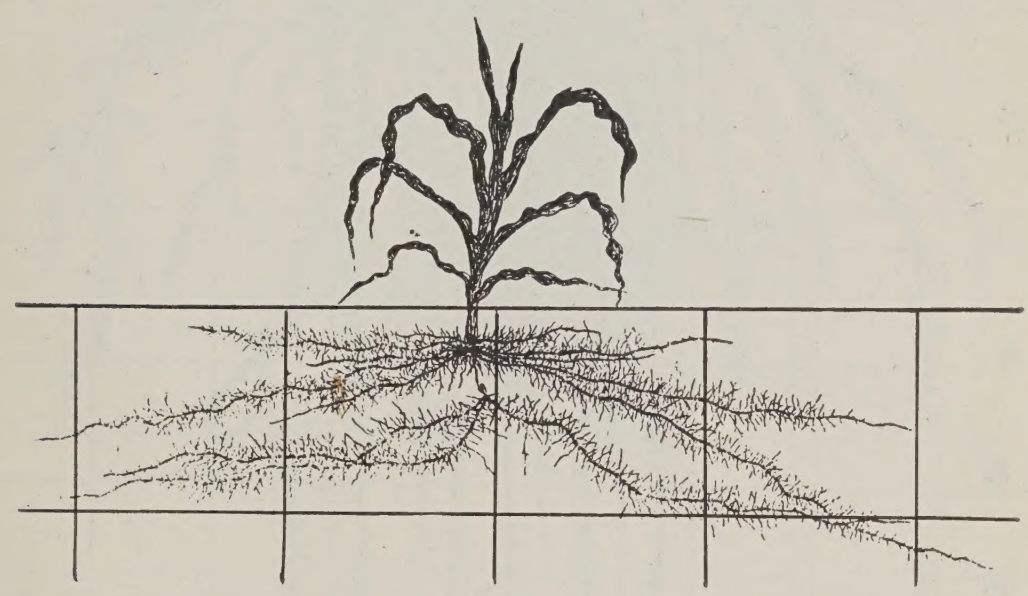


FIG. 19.—Root system of Iowa Silver Mine corn (*Zea Mays indentata*) 36 days old. Note the deeper primary and the upper secondary root systems. Cf. Fig. 20. (After Weaver.)

be seen the deeper primary and the shallow-feeding, secondary root systems. The shallower system completed its development early, so far as lateral spread is concerned, while the roots of the deeper system continued to increase in number and extent until the corn plant was mature.

A study of the root system of the potato (Early Ohio) at Peru, Nebraska, showed a "distinctly superficial" early growth. After the roots had grown out horizontally to a distance of 1 to 2.2 or more feet, they turned somewhat abruptly downward, leaving the subsoil area under the plant quite free from its own roots (Fig. 21). The maximum depth observed was over 3.5 feet (Fig. 22).

At What Depth Do Plants Absorb Water, and Nutrients?—In order to determine the amount of water and nutrients absorbed by native and crop plants from deeper soils Weaver and collaborators[1] grew the plants in cylindrical containers, made of galvanized sheet iron and plunged in the soil so that the plant grew under substantially normal crop conditions.

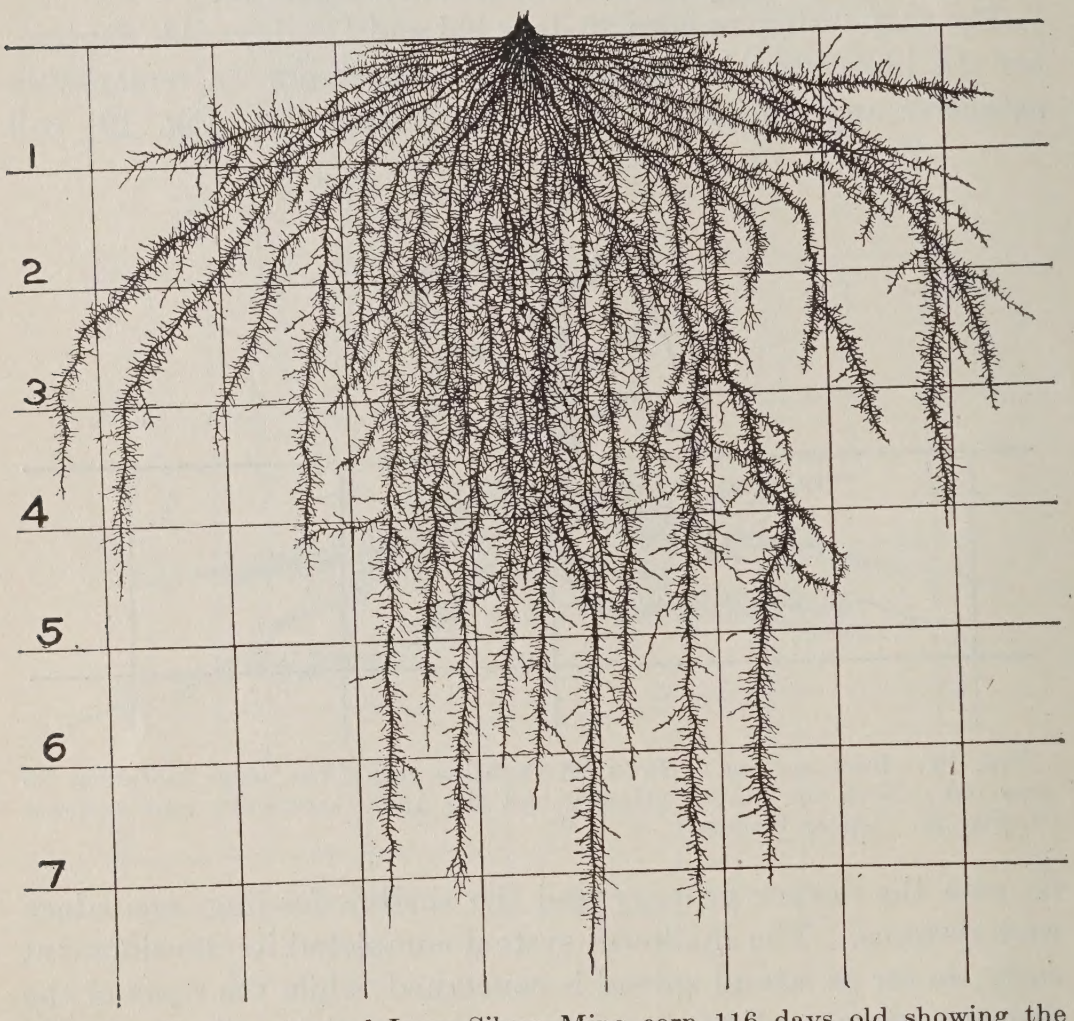


FIG. 20.—Root system of Iowa Silver Mine corn 116 days old showing the extensive development of the root system. Cf. Fig. 19. (After Weaver.)

"Preliminary experiments with oats showed that this crop absorbed water at all depths to 2.5 feet, even before blossoming. The amount of water absorbed by barley from the deeper depths

[1] Weaver (John E.), Jean (Franc C.), and Crist (John W.). Development and activities of roots of crop plants. Carnegie Inst. of Washington, Publication No. 316. Washington, D. C., May, 1922. The paragraph quoted above is from page 114.

(to 3.5 feet) is in direct relation to the growth of the root system into these deeper layers. The total amounts absorbed to depths of 2.5 feet were in general practically the same from the several 6-inch levels. Corn is an extravagant user of water, absorbing large quantities from the third and fourth foot of soil and smaller amounts from the fifth foot. Potatoes absorbed water to depths of 2.5 feet (approximately the limit of root extent), while the native grasses grown from transplanted sods, showed marked absorption to a similar depth."[1]

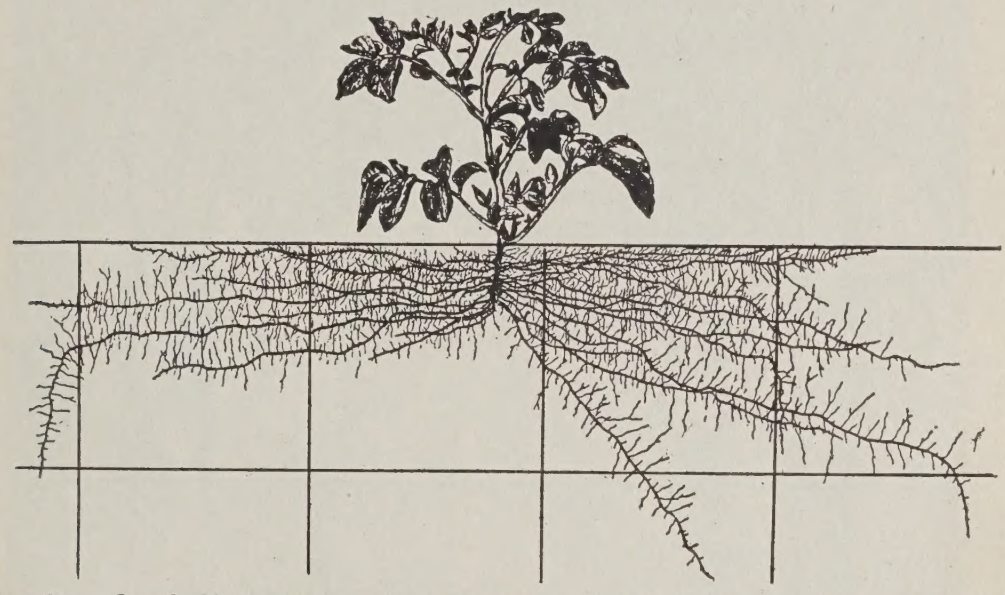


FIG. 21.—One half of root system of a potato plant 56 days old. (After Weaver.)

The results of these experiments are contrary to the view hitherto commonly held (but not based on careful experimental work), that plants absorb only from the top 6 or 8 inches of soil, and that the subsoil "plays only an indirect part in plant nutrition."[2]

The experiments just referred to also showed that roots were more abundant and more profusely branched in fertilized layers of soil, but such layers interfered with penetration to normal depths. It would follow from this that, if only the surface layers

[1] It should be noted that a plant that is an "extravagant" user of water (according to Weaver) may (according to Briggs and Schantz) have a low "water requirement." Compare the above statement for corn and potatoes with the table of water requirements (p. 31).

[2] Russell, Edward J. Soil conditions and plant growth. 3d Ed., p. 56. New York, 1917.

of soil are fertilized, the best root development would be in the region of little or no available water during drought, and this would be detrimental to crop-yield. It follows from all these studies that the deeper layers of soil are of large importance in the life of both cultivated and wild plants.

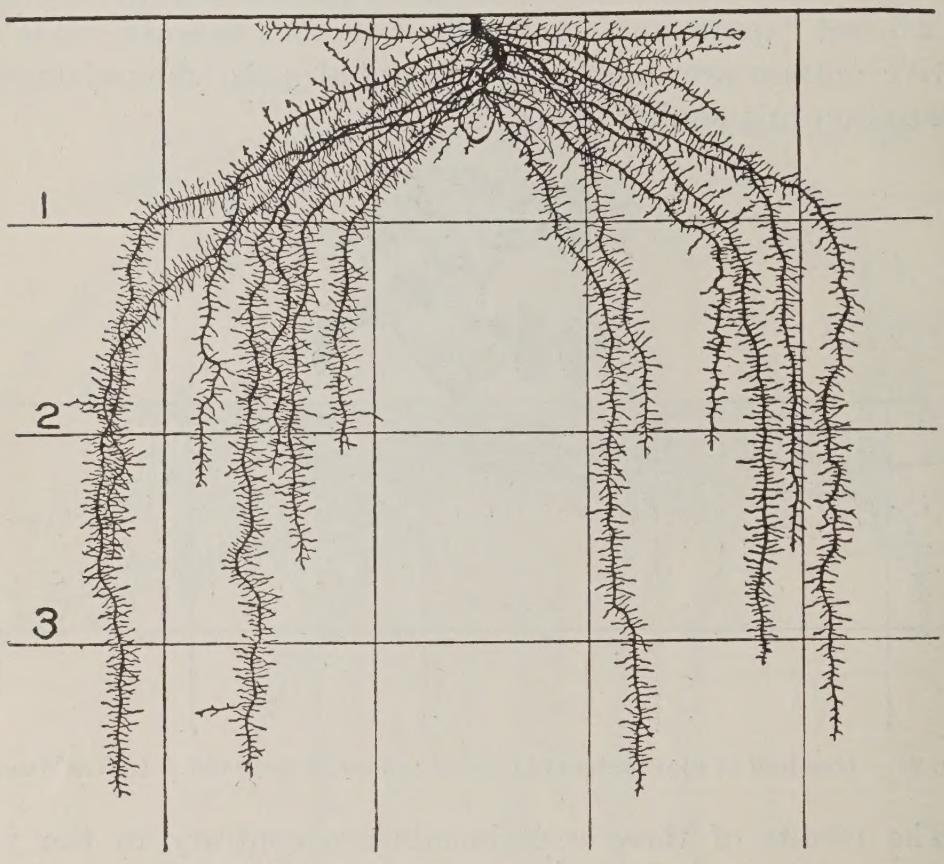


FIG. 22.—One half of root system of a mature potato plant. (After Weaver.)

Root-hairs.—Every amateur gardener knows that in transplanting the first essential is to keep the soil about the roots. No matter what other precautions are taken, if the soil falls away from the roots the plant wilts more readily after being transplanted. Moreover, if the soil is shaken or rubbed off, or if the bare roots are left exposed to the air too long the plant not only wilts, but recovery is very difficult, or fails completely. This is because, in the removal of the soil, certain innumerable, threadlike outgrowths of the surface of the root are torn away; when the bare root is exposed to the air they dry up. These are the *root-hairs*. Their preservation intact is thus seen to be necessary to the absorption of water from the soil. They are,

above all else, the most essential part of the root-system; without them (or some efficient substitute to take their place) the raising of crops would be quite impossible.

Zone of Root-hairs.—Root hairs may best be demonstrated to the naked eye in mass (Fig. 23). Flax seed or mustard seed are suitable to use for the purpose. An earthenware pan, such as is

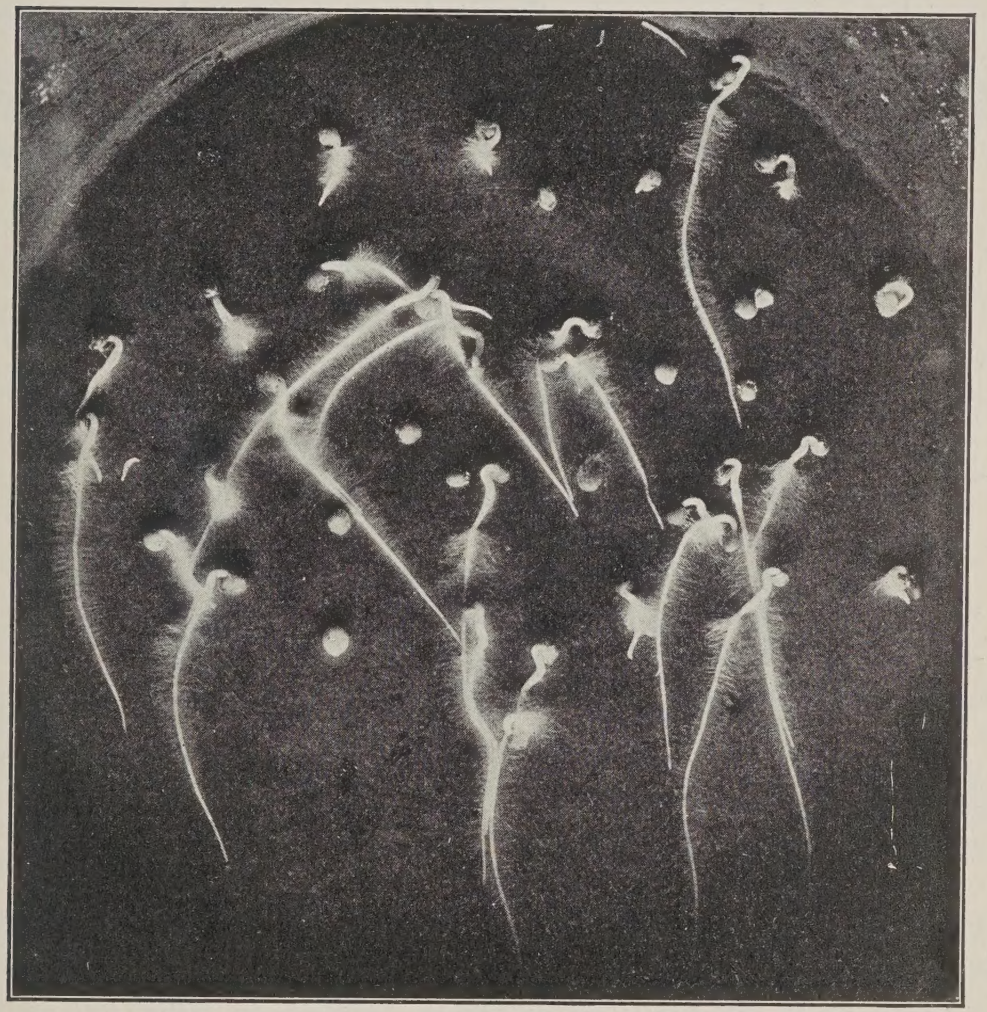


FIG. 23.—Germinating seeds of white mustard, showing development of root-hairs.

common in greenhouses, is thoroughly soaked in water and then imbedded in moist sand. A few seeds of the kind chosen are scattered over the surface, and the pan is covered with a glass plate. In 24–36 hours the seeds, if mustard, will have germinated, and the delicate, white root-hairs will appear against the darker background of the germinating dish.

It will be noticed that they occupy a definite zone which begins a short distance back from the tip of the root, and extends back towards, but never quite up to, the seed leaves. It will also be clearly seen that the longer and therefore older root-hairs are farthest back from the tip, so that the mass of them is more or less cone-shaped. On the roots of mature plants the zone of root-hairs is as well defined as on those of seedlings. Moreover, millions of root-hairs are being constantly produced, for each hair remains alive and active for only a few days.

Structure of Root-hairs.—When very thin sections are cut lengthwise of the root and mounted in water, the structure of the

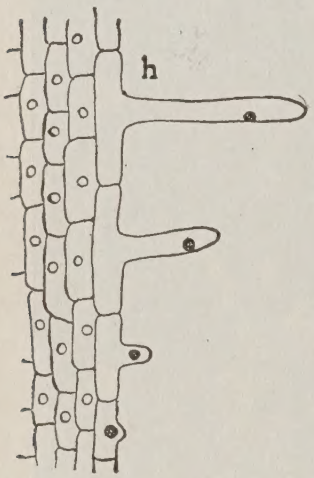


FIG. 24.—Diagram showing relation of root-hairs to adjacent cells of the root. *h*, the oldest of the four hairs shown, and furthest from the root-tip.

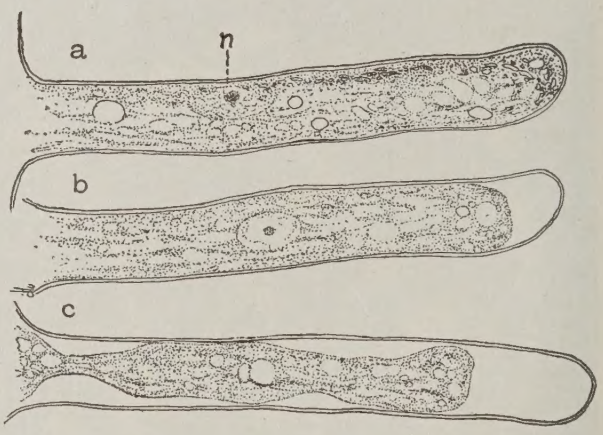


FIG. 25.—Root-hairs from the root of a mustard seedling. *a*, In state of turgor; *b*, beginning of plasmolysis after immersion in weak salt-solution; *c*, later stage of plasmolysis; *n*, nucleus.

root-hairs and their relation to the rest of the root may be studied under the microscope. By such an examination we find that root-hairs are really branches of external or *epidermal* cells of the root (Fig. 24). The hair and the remainder of the cells possess one continuous cell-cavity, containing one protoplast which more or less completely fills the cavity, especially in the younger hairs (Fig. 25). The nucleus is usually in the hair itself, and quite often near the tip. In very young cells, where the root-hair is just starting, the nucleus is usually found close to the region where the root-hair is beginning to develop. As in all cells, the protoplasm is saturated with the watery cell-sap. The

cell-walls have been found to consist of an inner layer of cellulose, and an outer layer of calcium pectate. These layers, of course, are not visible in fresh, living hairs. In "prepared" microscopic slides, where the tissues have been suitably stained, all of the parts above mentioned may be seen much more clearly.

Root-hairs and the Soil.—In order to understand how the root-hairs function in the absorption of water, we should first form a mental picture of their relation to the soil. It is well-known that soil can be too wet for plants, as well as too dry. It is a common experience, for example, for farmers to have a corn crop nearly or quite ruined by a long-continued inundation of

FIG. 26.—Diagram to illustrate a root-hair (*h*) in the soil, and its relation to the soil-particles, the capillary film of water (*w*), and the air spaces (*a*); *e*, epidermal cell of the root, of which the root-hair is an outgrowth, or branch. (After Sachs.)

the field; and in a field lying unevenly it is often seen that while the corn (and often other crops) does well on the higher, well-drained regions, it does poorly in the low-lying, over-wet places. Except for certain crops, such as rice, soil must be well drained in order to be suited to good crops. One of the reasons for this is that the roots, being alive, must breathe or respire, and if the spaces between the soil particles are completely filled with water, the air is expelled. A well drained soil is, at the same time, well aerated.

Now the root-hairs extend into the air spaces between the finer soil particles (Fig. 26). Though the soil is well drained

each soil-particle is moist, and has a layer of water all over its surface. This is the *capillary water*, so called because it moves along through the narrow spaces between the soil-particles by capillary attraction, similar to that which causes liquids that wet the surfaces of glass tubes to rise in tubes of small bore well above the level of the outside water in which the tubes are placed. Two opposing forces are here at work, the absorbing action of the root-hairs, and the capillary attraction in the soil. If a vigorous plant, growing in a flower pot, is left unwatered until it completely wilts, and a portion of the soil is then gently heated under a cold glass plate, it will be found that moisture is given off from the soil and condenses on the plate. By this simple experiment we learn that plants cannot absorb all the water from the soil. A condition is eventually reached where the capillary attraction of the soil particles for the film of water is greater than the absorbing force of the roots; when this condition is reached the plant will wilt unless the soil is watered.

FIG. 27.—Root-hairs, with soil-particles adhering. (After Sachs.)

When roots that have grown in soil are examined with the microscope the tiny soil-particles are seen to be imbedded in the walls of the root-hairs (Fig. 27). They are firmly held by *pectin mucilage*, formed from the layer of calcium pectate referred to above. This pectin is a colloid which has a great attraction for water, and is therefore of importance in connection with water absorption by roots.

How Root-hairs Absorb Water.—The walls of a root-hair, in contact with the moist protoplasm within and with the soil water without, are continually saturated with water; but the cell-wall is not the only barrier between the cell-sap and the soil-water; against the inner surface of the cell-wall is the lining

layer of cytoplasm, and this has at least three[1] distinct regions, viz. the limiting membrane or surface in contact with the cell-wall, the limiting membrane forming the wall of the vacuole or vacuoles, and the cytoplasmic substance between these two membranes. From the fact that the vacuoles are constantly filled with sap we infer that it does not readily pass through this fourfold barrier of cell-wall, membranes, and cytoplasm. How then does soil-water (containing in solution numerous soluble substances dissolved from the soil) pass in from without? In order to explain this we must understand the physical processes of *diffusion* and *osmosis*.

Diffusion.—With the diffusion of gases and of soluble substances in solution we are all more or less familiar. For example, if ordinary illuminating gas escapes from a leak or an open jet the odor of gas may soon be detected throughout the room or the entire house, and this would occur even if convection currents or "drafts" were quite lacking. The odor of a sweet-scented flower like the tuberose, or of a less pleasant substance like ether or chloroform, may also soon be detected in all parts of a room, even when the air is quite still. Such a result is due to the fact that the "odor" is matter in a gaseous state. As a result of the heat-energy which it contains, the particles (molecules) of a gas are in constant motion in straight lines until they collide with other particles, or with the walls of the containing vessel, when they bound off in another direction; thus the gas tends to distribute itself uniformly throughout all parts of the space to which it has access; this is the *diffusion of gases*.

When a soluble substance is dissolved it behaves in a somewhat similar manner, especially when the solution is very dilute, that is, the *solute* (substance dissolved), in very dilute solutions, becomes separated into its molecules, and the molecules into their constituent parts or *ions*, which are in constant motion in straight lines,[2] and tend to distribute themselves uniformly through-

[1] Osterhout has called attention to the fact that since the protoplasm is composed of a variety of structures (down to those which are ultramicroscopic) and each of these has a surface it is quite possible that many kinds of semipermeable surfaces, exist within the cell. (*Science* N. S. **38**: 408–409. Sept. 19, 1913.)

[2] The mean free path of the molecules and ions of a substance in solution, that is, the distance they may travel before colliding with other molecules or ions, is much shorter than in the case of a gas.

out the mass of the *solvent.* For example, let us imagine a glass tube inserted into a glass of pure water with the end of the tube reaching nearly but not quite to the bottom; further let us imagine this end of the tube temporarily closed by some device that will not permit any water to enter the tube. Let us now shove a small lump of sugar down the tube with a tightly fitting piston, and then open the lower end of the tube. The water will at once begin to dissolve the sugar, and if great precaution is taken to avoid currents or other motion in the water we shall, nevertheless, find in time that all parts of the water are equally sweet. The sugar has distributed itself by diffusion, its molecules moving in all directions, upward against the pull of gravity, and laterally as well as downward, as a result of their heat energy.[1]

Copper sulphate solution is heavier than water. If we take a tall glass beaker one third full of water we may insert a glass thistle tube to the bottom of the beaker and pour in under the water an equal quantity of copper sulphate solution, which is green in color. The water will rest on the surface of the heavier liquid, and the line of demarkation between the two will be quite well defined. Gradually however it will be seen that, without any stirring or shaking, the green color is beginning to appear in the lower part of the water, while at the same time the upper part of the copper sulphate is becoming lighter green; in fact, the two liquids are beginning to mix by diffusion, and if left long enough will become thoroughly intermingled so that each is evenly distributed in the space occupied by the entire mass of liquid.

Carbon bisulphide evaporates readily, it has a penetrating odor, and is also heavier than water. If a small amount, say 1 cc., is colored with iodine it may be poured into the bottom of a test-tube about two thirds full of water. It can be clearly seen at the bottom of the tube, but no odor can now be detected. In a short time the odor becomes noticeable at the opening of the test-tube, showing that the carbon bisulphide must have passed up through the water by diffusion, and evaporated from the

[1] The temperature of a solid, liquid, or gas is an expression of the rate of motion of its molecules. The energy manifest by this molecular motion is called heat. Thus it is that we say that the motion of the molecules of a substance in solution is an expression of heat energy.

surface. In time the odor will entirely cease, showing that all the carbon bisulphide has diffused upward to the surface and evaporated. These three experiments illustrate the diffusion of liquids.

Diffusion of a Gas through a Membrane.—A small sac or "balloon" of collodion is fastened air-tight to the end of a glass tube bent at right angles and extending horizontally. In the bore of the tube is placed a small drop of colored water. Evidently if the gaseous pressure within the tube is increased the bubble will move along in the direction of the arrow, away from the collodion sac. The sac full of atmospheric air which contains only a trace of the gas, carbon dioxide (CO_2), is now placed in a glass container, into which a quantity of carbon dioxide is then poured. Being heavier than air, the CO_2 may readily be poured, like water, and will replace a portion of the air around the collodion sac. Very shortly we shall see the drop of colored water begin to travel along through the tube, showing that carbon dioxide has begun to enter through the collodion wall, thus increasing the amount of gas inside and hence the gaseous pressure; in other words, we have demonstrated that the gas, carbon dioxide, can diffuse through a membrane.

Diffusion of Liquids through a Membrane.—It may be demonstrated by a simple experiment that diffusion of liquids can also take place through certain kinds of membranes. Thus, for example, a thistle tube, *f* (Fig. 28), is tightly closed at the large end by an imperforate piece of bladder membrane (*m*), and the bulb filled with a solution of cane sugar in water. The bulb is then immersed in tap water in a beaker. In the course of a few moments it may be seen that the liquid in the bulb is rising in the stem of the thistle tube. This can be explained only by the entrance of water through the substance of the membrane.

Studies in physical chemistry have resulted in different theories to account for this effect. The most generally accepted theory at present is substantially as follows. It is clear, from the condition and the result of the experiment just described that the membrane is so constructed that molecules of water, for example, can pass through, even in the absence of any openings large enough to be detected by the most powerful microscope; otherwise water could not have entered and raised the level of the liquid in the

thistle tube; since little, if any, sugar can be detected in the water outside the thistle tube it is evident that the molecules of sugar cannot readily pass through the membrane. As in the case of gases, the passage of the molecules was accomplished by their motion of diffusion due to their heat energy; but since there are fewer molecules of water per unit volume in the solution than in the pure water,[1] fewer molecules bombard the solution side of the membrane, and still fewer pass through; thus the passage of water is more rapid from the pure water to the solution, and with temperature and other conditions uniform, the process will continue until the weight of the column of liquid in the thistle tube exerts a pressure sufficient to counteract the tendency of the molecules of water to diffuse into the tube. Even when the liquids on opposite sides of the membrane are solutions of equal density, diffusion may continue, but, other conditions being equal, it will take place at the same rate in both directions and therefore the result will not be visible.

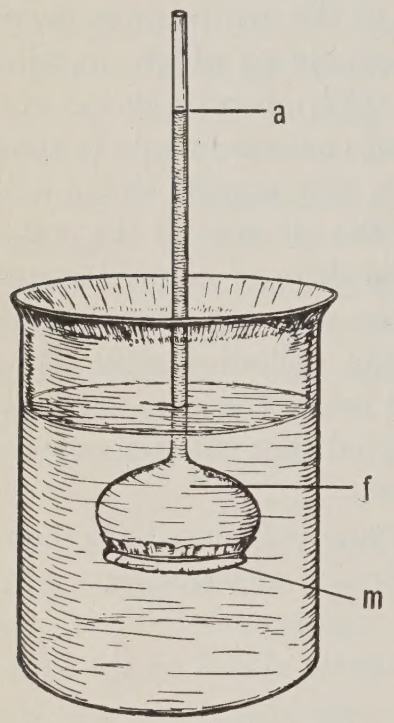


FIG. 28.—Experiment to illustrate osmosis. The beaker contains water. *f*, thistle tube, closed at the large end by a piece of bladder membrane, *m*. *a*, indicates the height of the liquid in the stem of the thistle tube.

Most porous membranes are, like the one used above, impermeable to the molecules of some substances, and are hence called *semi-permeable membranes.* Diffusion of gases or liquids through a membrane is called *osmosis.*[2] Solutions which can diffuse through semi-permeable membranes are called *osmotic solutions.*

In the case of the cell-sap of roots and the solution of various salts in the soil (often spoken of as "soil-water"), the osmotic condition is complex, since there are various diffusible substances dissolved in both liquids. Under such circumstances each solute behaves independently of all the others, diffusing through the

[1] Since a part of each volume of solution is occupied by molecules of the solute (sugar).

[2] From the Greek ὠσμός (*ōsmos*), pushing.

semi-permeable membrane most rapidly from the side where it is more dense to the side where it is less dense. At the same time another dissolved substance may, for the same reason, be passing through the membrane most rapidly in the opposite direction. A hypothetical case of this kind is illustrated in figure 29.

This is not the place to go deeply into a discussion of the facts and theories of osmosis; for this, a modern treatise on physical chemistry should be consulted. It is pertinent, however, to note here the necessity of avoiding several misconceptions with

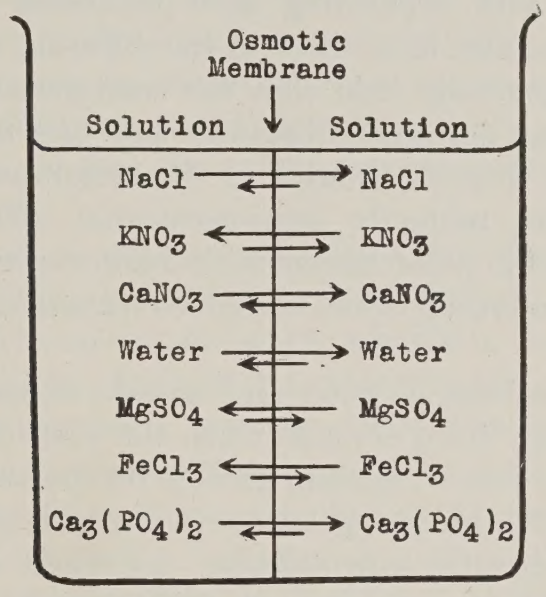


FIG. 29.—Diagram to illustrate the independent osmotic behavior of various salts when dissolved together in the same solvent. The pairs of arrows indicate osmotic passage in both directions through the membrane, and the longer arrow of the pair indicates the more rapid passage of the salt from that side of the membrane where it occurs in denser solution to the side where it is less dense.

which the literature of botany is full. Van't Hoff[1] showed that for ideal (*i.e.*, infinitely dilute) solutions the solute behaves like a gas, and the same law applies as for the diffusion of gases. By a too loose logic this principle has been extended in statement as applying to solutions and osmosis in general. Thus we read much of "osmotic pressure," as though that were an actual physical effect produced on the semi-permeable membrane by its bombardment by the molecules of the liquid. It has also been commonly stated that semi-permeable membranes act like a sieve, preventing the passage of certain solutes because

[1] J. H. VAN'T HOFF (1852–1911), a celebrated Dutch chemist, noted for his brilliant contributions to the physical chemistry of solutions.

their molecules were too large to penetrate the ultramicoscropic meshes of the membrane.

In it now generally recognized in physical chemistry that these ideas are quite erroneous. Osmotic pressure is not considered an actual physical pressure against the membrane that separates a solvent and solution, but merely as the measure of the pressure that would have to be exerted on the solution to completely stop the diffusion of the solvent into it through the membrane. The physical and chemical forces acting in an *osmotic couple* (solvent and solution with separating semi-permeable membrane) are much more complex than those in the diffusion of gases, and the view is now generally held that the semi-permeable membrane acts as a solvent, and that substances may pass through by osmosis only when they are soluble in the membrane. Few, if any, membranes are perfectly semi-permeable, allowing only the solvent to pass; in plant tissues most membranes show a selective permeability allowing some dissolved substances to pass, but not others.[1]

Substances soluble in water and capable of osmosis are *crystalloids*, since they form crystals when the solution is evaporated; substances like starch, calcium pectate (in the outer layer of some cell-walls, p. 43), tannin, gelatine, etc., which swell up in water but will not dissolve, are *colloids*. As noted in the preceding chapter, colloids osmose not at all, or only very slightly.

Application to Root-hairs.—The application of the principle of osmosis to root-hairs in the soil has, no doubt, already been made by the thoughtful reader. It is seen at once that the conditions in nature are not as simple as in the experiment. The solutions involved are the cell-sap and the soil-water. The sim-

[1] The electrical conductivity of pure water is very slight; its conductivity increases with the number of units (molecules and ions) of dissolved substances (electrolytes) present. The impermeability of the protoplasm of the yeast plant, for example, is shown by the experiments of Paine (Proc. Roy. Soc. B **84**: 289–307. 1911), who found the electrical conductivity of the cell-sap of brewer's yeast from beer indicated by the figure 742, while the conductivity of the beer was indicated by the figure 146, showing how impermeable the cell-membranes were to the substances dissolved in the cell-sap. Dixon and Atkins (Proc. Roy. Dublin Soc. N. S. **12**: 275–311. 1910) found that water secreted in drops from the leaf tips of *Colocasia antiquorum* was almost as pure as Dublin tap water, described as very pure and soft.

ple membrane of the experiment is replaced in the root-hair by the complex lining layer of protoplasm, which opposes at least two (and possibly several) semi-permeable membranes between the cell-sap and the soil-water solution. Moreover the liquids must first soak through the cell-wall by the process known as *imbibition.* In addition, the cell-sap and the soil-water are both complex solutions of various substances. But, notwithstanding the complexity of the conditions, the process is largely that of osmosis. In fact, it may here be remarked that plants can take in nothing solid; the only condition in which matter can enter a plant from without is in the liquid or gaseous state, or in solution; and the only process by which it can enter an uninjured plant is by gaseous diffusion or by osmosis. Since water is absolutely necessary to life, the great importance of osmosis may readily be inferred.

Turgor.—It will be readily understood that if water continues to pass into a cell by osmosis, and is not removed as rapidly as it enters, there will be an accumulation of liquid in the vacuoles, and considerable internal hydrostatic pressure will be developed. That this is what occurs may be easily demonstrated. If a sausage is placed in warm water it gradually swells up, and often becomes so distended that, when pricked with a pin, a jet of water will be forcibly expelled. In a crude way the sausage represents a plant cell. A similar thing is illustrated by the little sacs of "juice" in an orange. It is this internal pressure that keeps the lining layer of cytoplasm closely appressed to the cell-wall, as it is seen to be whenever healthy, uninjured cells are examined under the microscope. In fact, the internal pressure usually becomes so great as to distend or stretch the slightly elastic cell-wall. Such a condition of the cell is called *turgor;* the cell is said to be *turgid.* When all or most of the cells of a tissue are in a state of turgor the tissue is turgid or in a state of rigidity. We are familiar with numerous illustrations of this. For example, a new potato is turgid and rigid, while an old potato, though uninjured, has lost water by evaporation and is soft and flabby; stalks of rhubarb, when freshly picked, are stiff and even brittle, but after they have lain in the market, out of water, they are easily bent without breaking; kernels of fresh sweet-corn on the cob are distended and smooth, but finally become shrunken and wrinkled.

Plasmolysis.—If a cell which has lost its turgor is examined under the microscope the protoplasm will be seen to have more or less shrunk away from the cell-wall; for that reason the cell is said to be plasmolized, or in a state of *plasmolysis.*[1] The condition may be easily produced by irrigating a turgid cell with a solution more dense than the cell-sap. If fresh root-hairs or a fresh leaf of *Elodea* are mounted in water on a microscopic slide the cells will be found turgid (see p. 14). If they are now irrigated with a 5% solution of common table-salt the protoplasm will gradually shrink away from the cell-wall, and the protoplast will tend to assume a spherical shape. The explanation of this is that a process the exact opposite of absorption has taken place; *exosmosis* is more rapid than *endosmosis*, and the amount of liquid in the vacuoles is diminished. At the same time the salt solution passes through the cell-wall faster than it does through the lining layer of cytoplasm, and accumulates between the wall and the protoplast, thus loosening (plasmolyzing) the plasma from contact with the wall. When the cells of a tissue are plasmolyzed turgor ceases, and the rigidity of the tissues is lost.

Conditions of Water Supply.—As in most life processes, the rate of supply of water to plants depends upon two sets of conditions—the external and the internal. The principal external conditions controlling water supply are,

1. The extent of the root-system, which depends upon the rate of growth of the roots.

2. The rate at which the soil can deliver water to the plant, which includes, not only the release of the water in direct contact with the roots, but also the rate at which water from a distance can travel toward the absorbing roots (by capillary action). This depends largely upon the physical character of the soil, especially the distance apart of the soil particles, and the amount of water present, together with numerous other conditions. These facts underlie certain agricultural practices.

The principal internal condition is the rate at which water is transported, used, and given off. The rate at which water is given off is again controlled in part by the humidity and other conditions of the surrounding air, such as temperature and wind.

[1] From two Greek words, *plasma* and *luein* (meaning to loose, or set free).

CHAPTER IV

LOSS OF WATER. TRANSPIRATION

The Amount of Water Given Off.—In the preceding chapter we have had occasion to refer to the commonly known fact that plants not supplied with sufficient water wilt, because they are constantly losing water by its evaporation into the air. Figures of the amount of water given off by certain plants have already been given (p. 31). The following additional examples are cited by Selina Gaye.[1]

FIG. 30.—*Aster sp.*, showing transition from petiolate, through petiolate-stipulate, to sessile leaves. Note the elongation of the lower petioles, thus bringing the blades out to better light exposure.

A grass plant gives up its own weight of water in twenty-four hours, in hot, dry weather; and a square foot of turf will yield more than $1\frac{1}{5}$ pints of water in this time. But a square foot of long pasture-grass gives off nearly $4\frac{2}{5}$ pints, or as much as 106 tons of water to the acre. An acre of oats gives off several hundred tons of water in one season.

The leaf-surface (upper and under surfaces) of a sunflower plant three and one-half feet high was found to be 32 square feet, and the loss of water from one such plant was a pint and a half during a day of twelve hours. A cabbage having leaves that,

[1] Gaye, Selina. The great world's farm, pp. 102–104. London, Seeley & Co., Ltd., 1894.

if opened out, would cover only nineteen square feet, was found to give off two and one half pints in twenty-four hours. Hales, one of the founders of plant physiology, calculated from careful experiments that an average crop of cabbages would lose from three to four tons of water a day per acre.

A medium sized elm tree was found to have about 7,000,000 leaves with a total surface of five acres; from the surfaces of these leaves about seven and three-quarters tons of water evaporated in

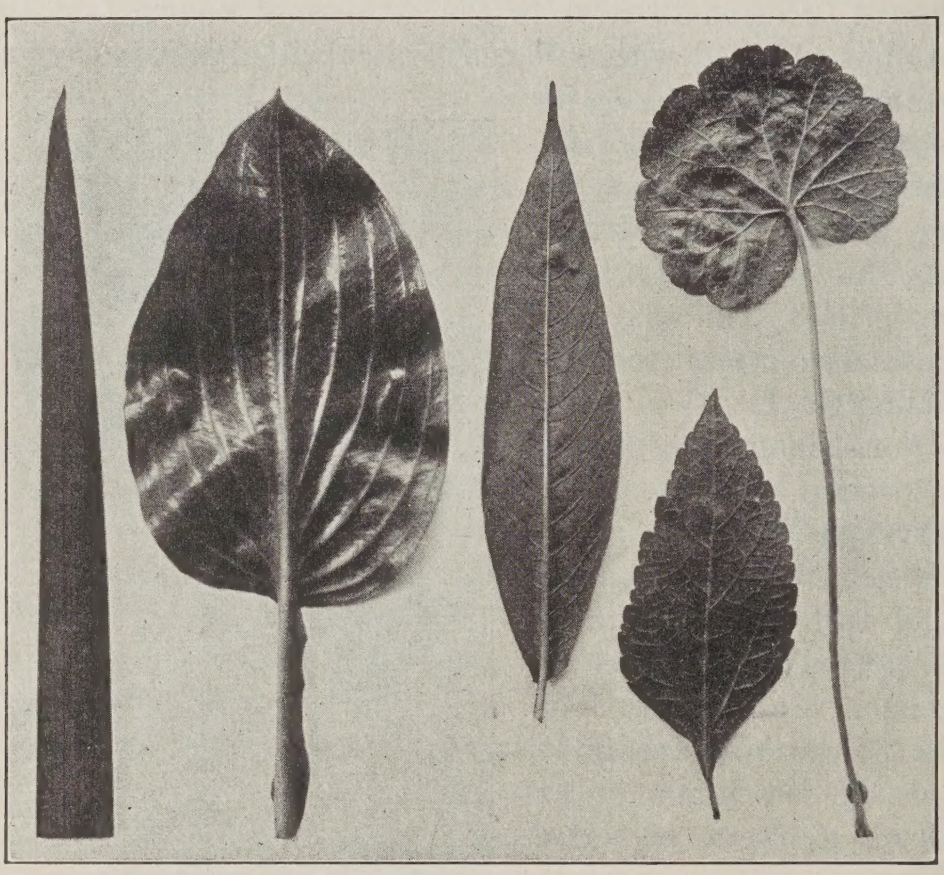


FIG. 31.—Various types of leaf-blade.

twelve hours of clear, dry weather. Gaye exclaims, "if this is the quantity [of water] returned to the air by a single tree of only moderate size, how large must be the amount received from a wood or forest, containing hundreds of thousand of trees!" Such a calculation has been made for the beech; an acre of large beech trees, on the basis of figures obtained by von Höhnel, will give off by transpiration more than 30,000 barrels of water in one summer.

How Water Is Lost from Plants.—As every gardener knows, the chief organs involved in the loss of water from plants are the

leaves. On the knowledge of this fact are based numerous practices in gardening. For example, when young plants, such as cabbage, are transplanted in the spring, the larger leaves are pinched off; this reduces the loss of water until the roots become reestablished in the garden soil. In order to understand the mechanism of water-loss, therefore, it is necessary to know the finer structure of a foliage leaf.

FIG. 32.—Leaf of a banana (*Musa sapientum*), showing enormous development of the blade, and also how easily a leaf-blade may be torn in the absence of a marginal vein. This leaf-blade (*i.e.*, without the petiole) measured over 15 ft. long and 3 ft. wide, thus exposing over 45 sq. ft. of green tissue to the light.

The Structure of a Foliage Leaf.—The principal parts of a foliage leaf have been noted in Chapter I. There are many—almost innumerable—variations of the general plan or structure there described. Any one of the principal parts—blade, petiole, stipules—may be greatly modified, or they may be entirely wanting. Blade and stipules may be present in the first leaves, or in the early stages of all leaves, and lacking in later leaves or in later stages. Stipules and petiole may both function as blade; when both are wanting the leaf is said to be *sessile*. Again, the

blade may be simple in the embryonic or the next following leaf, and compound in subsequent leaves, as in the bean. The margin of the blade may be entire, serrate, notched, wavy, incised, and all of these in varying degrees. The apex and base of the blade may be pointed in different ways, or either may be more or less incised, or appearing as if cut squarely off (*truncate.*) Some of these innumerable variations are illustrated in figures 30–35.

FIG. 33.—Leaf of Hercules club (*Aralia spinosa*), partly thrice compound. The leaf-blade measured 15 in. wide at the base, and 12 in. long.

The different external features of leaves serve as characters which help us to distinguish the different species and varieties of plants. Some of these characters are significant in relation to function, but from the standpoint of relation to water and light it is above all important to note that, whatever other characteristics it may have, the leaf is essentially a flat, expanded, and green organ.

The Tissues of a Leaf.—If we take almost any vigorous, mature, green leaf, it is easy to show that each surface is covered with a delicate, thin membrane—the *epidermis*, which may be peeled off in portions (Fig. 36). This is almost entirely—sometimes wholly—devoid of green color. It may or may not bear *hairs*. Between the upper and the lower epidermis is the green mid-leaf tissue, or *mesophyll*, sometimes called "*leaf-parenchyma*." Through the mesophyll the veins extend, forming the *vascular system* or circulatory system of the leaf.

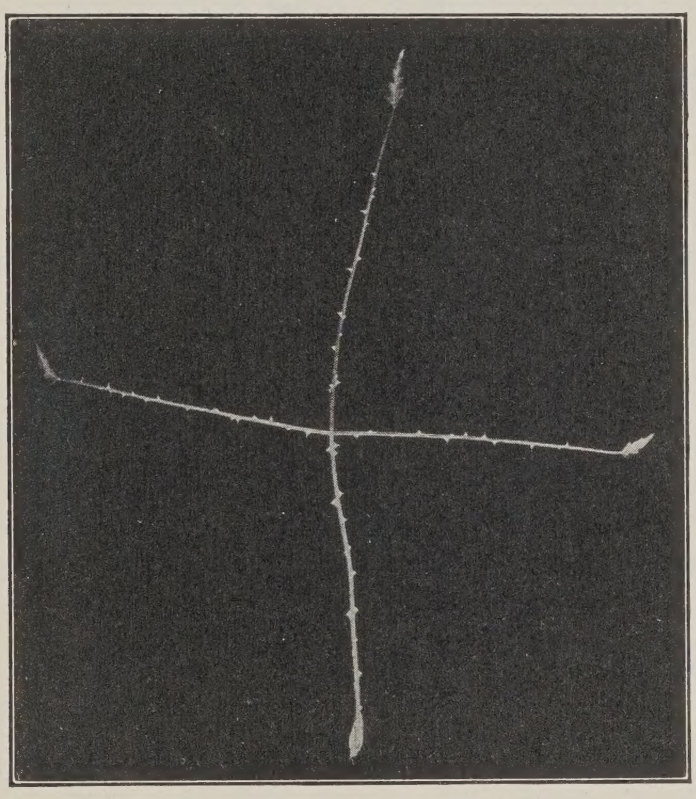


FIG. 34.—New Zealand raspberry (*Rubus australis*). The lower portion is the petiole; the blade is reduced to three spiny veins, with slight development of the blade at the tips.

Microscopic Structure or Histology. 1. *Upper Epidermis.*—If a portion of the upper epidermis of a lilac leaf is mounted in water and examined under the low power lens of the microscope, it is seen to be composed of cells of irregular shape, having no green coloring matter. Frequently a nucleus may be seen in one or more of the cells (Fig. 37).

2. *Lower Epidermis.*—If a portion of the lower epidermis is examined in a similar way it will be found to resemble the upper

epidermis, except for the presence of numerous little lunar-shaped cells, containing green coloring matter, and occurring in pairs, each pair surrounding a tiny hole (Fig. 37). The hole is called a *stoma* (plural, *stomata*), and the lunar-shaped cells are the *guard cells* of the stomata. In the leaves of some species (*e.g.*, the potato, *Tropaeolum*, corn, and others—Fig. 38) there are stomata in both the upper and lower epidermis, though commonly they are fewer in number in the upper epidermis. In other species,

FIG. 35.—*Acacia melanoxylon*. Branch showing variation in leaves from petiolate leaves with twice compound blade to leaves without blades, the flattened petiole being modified to function as a blade.

and notably in those with leaves that float on water, there are stomata only in the upper epidermis, which is the only surface directly exposed to the air. Underneath each stoma is an *air-chamber*.

Number of Stomata.—The number of stomata in the leaves of even a small plant, such as beet or corn, is prodigious; the number on a large tree is quite beyond our comprehension. For example, it has been estimated that a medium sized apple leaf

may have as many as 400,000 stomata, but they occur only in the lower epidermis of apple leaves, while in most plants they occur on both sides of the leaf. Many leaves must possess more than one million, not to mention such extra large leaves as those of squash or the enormous leaves of the banana. But the stomatal openings are tiny, and when fully open their total area would not be more than one one-hundredth the area of the leaf surface.

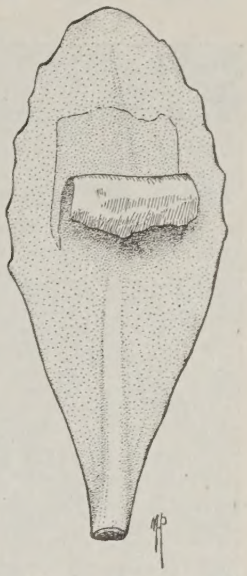


FIG. 36.—Leaf of a live-for-ever (*Sedum* sp.), with a portion of the epidermis peeled back. Underneath the epidermis is the mesophyll.

3. *Hydathodes.*—The leaves of many plants, including, for example, the potato, corn (*Zea Mays*) and other cereal grains, nasturtium (*Tropaeolum*), *Primula*, poppy, bean (*Phaseolus*), and others, possess organs whose primary function is the secretion or (as the case may be) the absorption of water. For this reason they are called *hydathodes.*[1] The hydathode includes an opening or *water-pore* through the epidermis which resembles an ordinary stoma except that usually it is larger and the guard-cells have no power of opening and closing (*Cf.* p. 768). Underneath the water-pore the cells are usually organized into a more or less

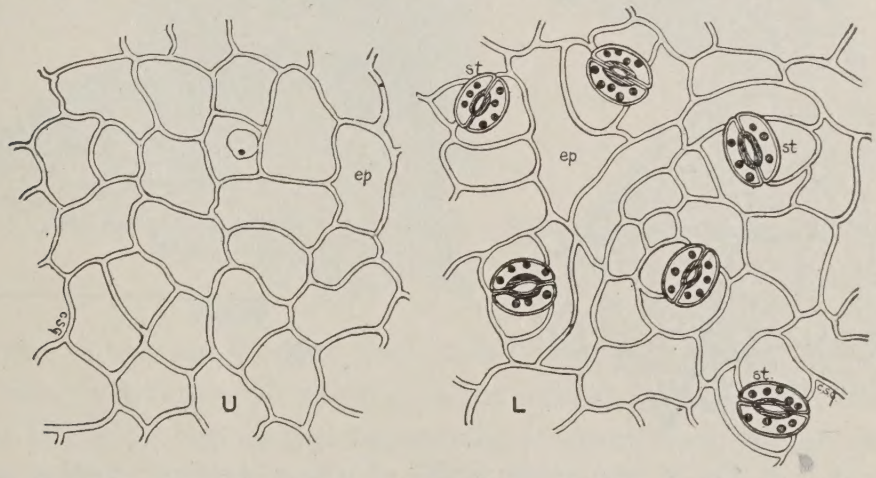


FIG. 37.—Lizard's tail (*Saururus cernuus*). Portions of leaf-epidermis; *U*, upper epidermis; *L*, lower epidermis; *ep*, epidermal cell; *st*, guard-cells of the stomata. (Camera lucida drawing.)

simple glandular tissue, which communicates with the veins.

[1] From the Greek ὕδωρ (*hydor*), water + ὁδός (*hodos*), way, meaning that the hydathodes afford a way for water.

There is usually an air chamber directly underneath the water-pores (Figs. 39–41). Some plants (*e.g.*, *Primula*, *Fuchsia*, and

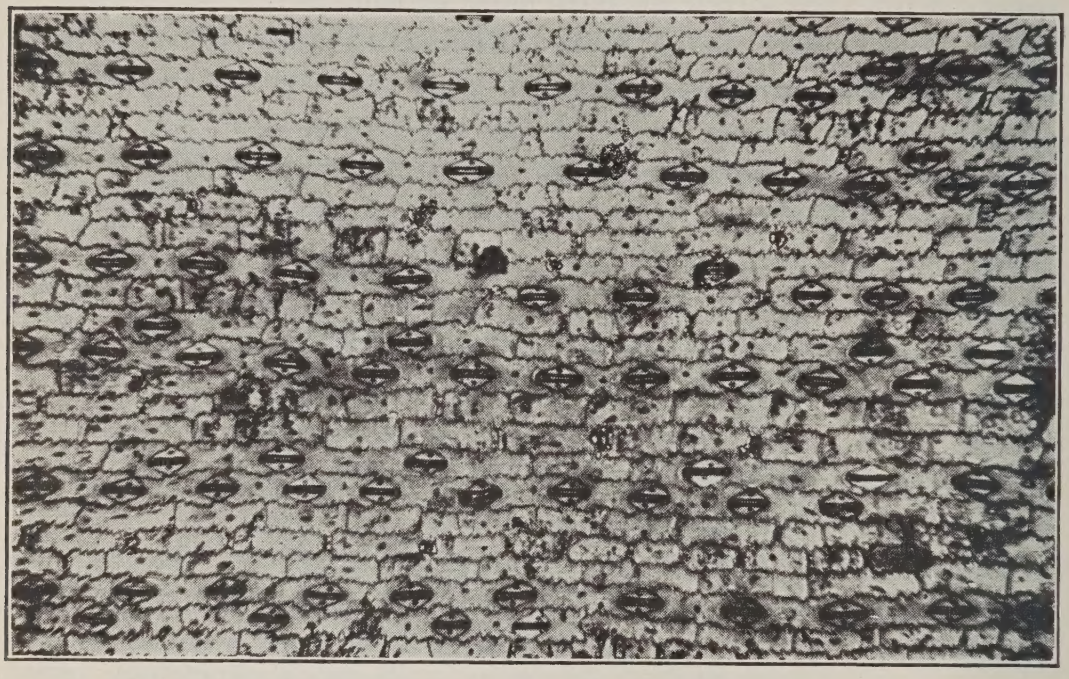


FIG. 38.—Indian corn (*Zea Mays*). Photomicrograph of a portion of leaf epidermis having an area of 0.83 sq.mm., showing the stomata and other epidermal cells. (After Kiesselbach.)

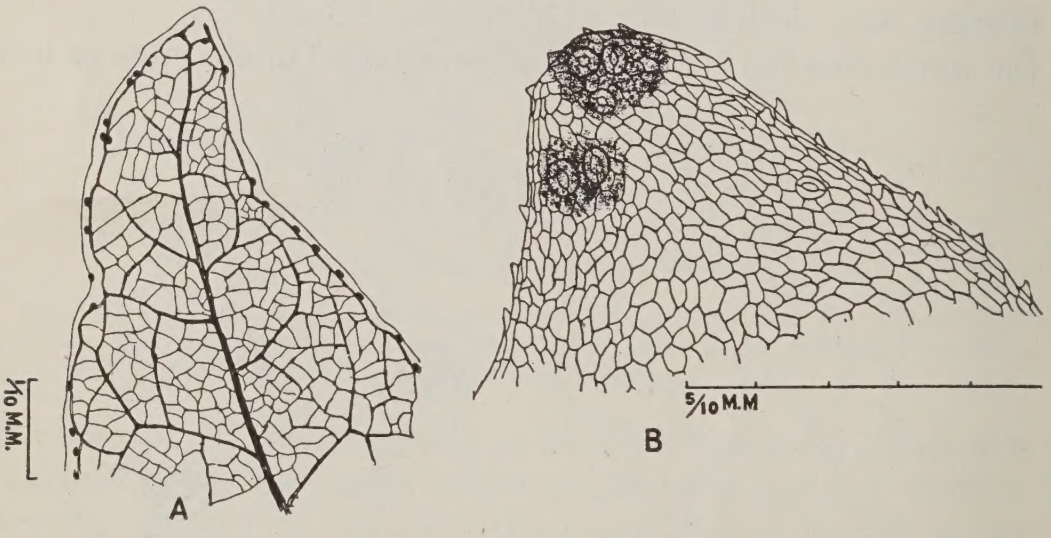


FIG. 39.—*A*, Tip of very young leaflet of potato showing venation and the location of the hydathodes along the leaf-margin. *B*, Tip of mature leaflet in surface view, showing groups of hydathodes. Dead tissue under the pores is indicated by the shading. (After Lutman.)

others) have only one water-pore for each hydathode; others (*e.g.*, Elm, *Crataegus*, and others) may have 3–6 pores for each hyda-

thode. Some plants (*e.g.*, *Delphinium* and others) have a water-pore at the tip of each tooth of the leaf-margin.

The word hydathode was introduced into botanical literature by Haberlandt, and he describes the apical pores at the leaf-tips of many monocotyledonous plants (*e.g.*, grasses and their relatives) as a peculiar type of hydathode. In such cases there is, at the end of the midrib, a tiny depression formed by the disinte-

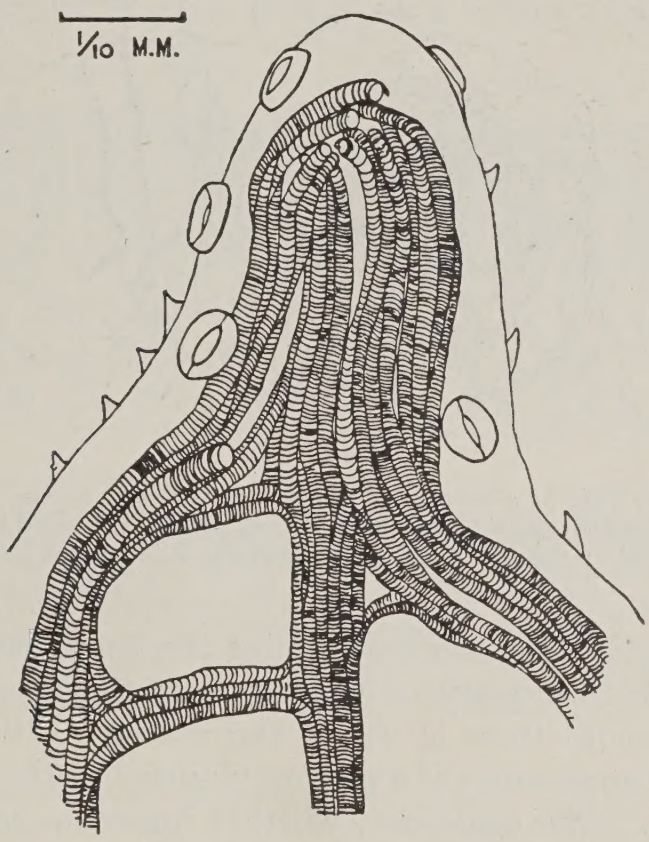


FIG. 40.—Tip of potato leaflet (enlarged). Showing hydathodes and the network of vascular bundles. (After Lutman.)

gration of the epidermal and sub-epidermal cells. Tracheids from the vascular system project into these depressions, thus, in effect, bringing the water-conducting system clear to the surface of the leaf.

Hydathodes are common in plants of humid tropical regions, and enable the plant to get rid of water (by secretion) when the air is so humid as greatly to reduce or stop transpiration. The drops of water secreted by the grass leaves on a lawn may fre-

quently be seen, especially in early morning where the sun has not yet shone, or at night after sunset.

The leaves of beans have on the underside short, curved hairs which act as hydathodes. The liquid secreted is not pure water but contains solid substances in solution. Hydathodes may become transformed into digestive glands or (as in *Colocasia*) into nectaries.

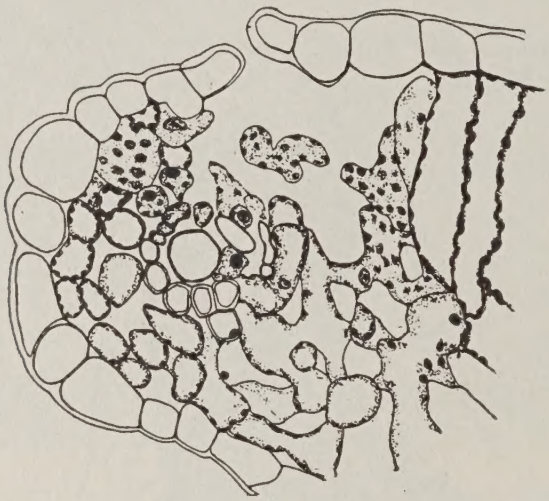


FIG. 41.—Drawing of a section of potato leaf as seen under the microscope The section passes through a hydathode and shows the pore and the air-chamber beneath, enclosed by the cells of the somewhat glandular tissue. (After Lutman.)

4. *Mesophyll.*—In order to examine the finer structure of the mesophyll it is necessary to cut extremely thin *cross-sections* of the blade, mount these in water, and examine with the microscope. The appearance of a portion of such a section is shown in in figure 42. The epidermis, whether upper or lower, is seen to be a layer of cells only one cell thick; their longest dimensions are parallel to the surface of the leaf. The outer cell-walls of the epidermal cells are usually covered over with a waxy substance, the *cuticle*, secreted by the protoplasm of these cells. Water does not readily pass through the cuticle, as it does through the cell-walls; nor can the cuticle easily be wetted, with water. If a fresh green leaf of this type is immersed in water the surface looks silvery under the water; this is because of a layer of air between the water and the leaf surface; when the leaf is withdrawn it is seen not to be wet. The epidermal cells are alive and active, for the protoplast may be observed within, but,

though the leaf is green, it is seen here, also, that there is no green color in the epidermal cells, except the guard cells, which possess chloroplasts.

At frequent intervals in the section we find the tiny stomata, or holes, through the epidermis, surrounded by the two guard cells, each with its green bodies or *chloroplasts*. When the guard cells are turgid they expand somewhat, and in such a way that the stomatal opening becomes larger; with the loss of turgidity (when the supply of water falls below a certain point, and espe-

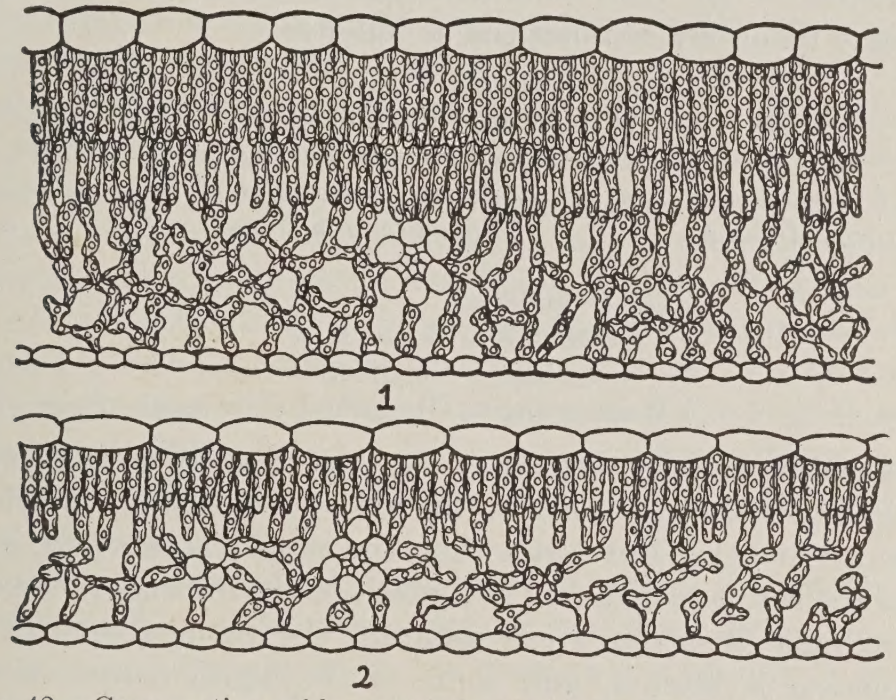


FIG. 42.—Cross-sections of leaves of an oak (*Quercus novimexicana*), showing the effect of different light conditions on the internal anatomy. 1, from leaf growing in sunlight; 2, from leaf growing in the shade. (After Clements.)

cially when the leaf wilts) these cells shrink together in such a way as to more or less completely close the stomata.

The mesophyll appears prominent because each cell contains so many chlorophyll bodies. This tissue is seen at once to be *differentiated* into two quite distinct portions. The cells lying directly under the upper epidermis are of fairly uniform size and shape, and lie close together in contact, with their long axes more or less at right angles to the leaf surface (Fig. 42). This is the *palisade layer* or palisade parenchyma, so named from the arrangement of the cells.

Between the palisade layer and the lower epidermis the mesophyll cells are of irregular shape and size, and lie in irregular positions, with generous spaces between. This is the *spongy parenchyma.* The intercellular spaces are larger than the cells, and it is seen that the stomata always open into one of these intercellular spaces. The arrangement of the cells in palisade and spongy parenchyma makes it quite clear why the upper surfaces of leaves are commonly of a darker green color than the under surfaces. The structure of the leaf-veins will be described in Chapter V (p. 75). The histological features of the foliage leaf may be briefly summarized as follows:

Leaf blade
- Upper epidermis
  - With or without stomata
  - Sometimes with epidermal hairs
- Mesophyll
  - Palisade parenchyma
  - Spongy parenchyma
- Veins
- Lower epidermis
  - Commonly with stomata
  - Sometimes with epidermal hairs
- Water-stomata (Hydathodes), in some species

Transpiration.—Let us see, now, just how it is that water supplied by the roots is lost to the air by the leaves. When the water is not being lost faster than the supply is renewed, every cell of the leaf is turgid, and as a result of the internal pressure of the cell-sap (resulting from osmosis) the permeability of the protoplasm is altered, and some of the liquid passes through the cell-wall to the outer surface. Here it evaporates into the intercellular spaces, with the result that the air in these spaces is normally *saturated* with water vapor; that is, it contains all the water vapor possible at the existing temperature and atmospheric pressure. When, as is commonly the case, the humidity of the air outside the leaf is less than that of the intercellular spaces, the water vapor diffuses out through the stomata; here it may either continue to diffuse into the air, or it may, under certain conditions of atmospheric temperature and humidity, condense on the surface of the leaf (often in drops forming "dew") and later evaporate into the air. The diffusion of water vapor through the stomata is called *transpiration.* It has been found that, in certain plants and under certain conditions, water may

pass through an epidermis (with its cuticle) devoid of stomata, and then evaporate into the air. By an extension of terms this is called *cuticular transpiration*, as distinguished from *stomatal transpiration*.

Control of Transpiration.—From what has been said in the preceding paragraph it will be seen that the rate at which water vapor can pass from within a leaf to the surrounding air depends, in part, upon the readiness with which it may diffuse or evaporate into the air, and this in turn depends upon the degree of humidity of the atmosphere in contact with the leaf. It is evident that, other conditions being equal, transpiration will be more rapid on warm, windy days than on cool, quiet days, in sunshine than in shade, during daytime than at night, near the tips of branches (in trees) than in toward the trunk, with isolated trees in a meadow than with trees in a dense forest, in exposed than in sheltered situations, on mountain summits than in valleys, in deserts than in swamps and marshes, and so on. It is also clear, in this connection, why it is an advantage for plants just transplanted to be covered over with a paper or a box, for this tends to increase the humidity of the surrounding air and thus lessen evaporation and .transpiration. For a similar reason florists, when wetting down plants, thoroughly sprinkle the ceiling and side walls of the greenhouse.

But transpiration is not controlled merely by external factors; it may also be regulated to a certain extent by the action of the plant, such, for example, as the opening and closing of the stomata above referred to (p. 58). A simple experiment will illustrate the fact that the presence of stomata facilitates transpiration. A piece of filter paper or thin blotting paper, soaked in a solution of cobalt chloride, is blue in color when quite dry, but turns pink when moistened. A leaf is chosen that is known to have fewer stomata on the upper than on the under side—or, better yet, one that has no stomata on the upper side. The leaf surface must be dry. A small piece of perfectly dry cobalt paper is now placed against each surface of the leaf, which is then fastened between two pieces of glass with rubber bands. The preparation should be examined at frequent intervals. After a period, depending on the kind of leaf used and the external conditions, it will be seen that the cobalt paper next the lower epidermis

begins to turn pink much more quickly than the piece next the upper epidermis, showing the more rapid transpiration from the lower surface of the leaf.

Studies of transpiration of two desert plants, the ocotillo (*Fouquieria splendens*) and a verbena (*V. ciliata*), in the Arizona desert, by Lloyd, seem to indicate that there is not as close a regulation of the process by the stomata as was formerly thought, *e.g.*, by Darwin, who worked with ivy (*Hedera helix*) and laurel (*Prunus laurocerasus*) in the humid climate of England.

Gray and Peirce, in 1919, studied the stomatal action in wheat, oats, rye, barley, and wild oats (*Avena fatua*), and found that, in the intermediate climate of Southern California, the stomata of these plants open with light and close with darkness. This would, of course favor the passage of water-vapor and other gases by day, and retard it at night. There appears to be no necessary or uniform relation between the number of stomata or the total area of the stomatal openings and the amount of water transpired; the loss of water is apparently regulated by a combination of internal and external factors, among which the stomata are less important than was previously supposed. This subject will be treated more fully in Chapter VI, but it should be noted here that the loss of water by transpiration from living plants is a very different process from the "drying up" of dead plants. The latter is merely by evaporation, and the tissue can part with all of its water. We are familiar with the *dry* dead leaves in autumn; but a living plant or organ cannot lose all of its water by transpiration. It is instructive in this connection to make a very simple experiment. Choose two equally vigorous foliage leaves from a plant; kill one leaf by immersing it in hot water, then lay the two leaves side by side uncovered in the room. Although the leaf that was killed was, in the process, thoroughly wetted by the water, it will be found that it becomes perfectly dry and brittle within a few hours, while the other leaf remains soft and only wilted, and may even become turgid again if the leaf-stalk is placed in water and transpiration is checked by covering the leaf with a bell-jar.

Effect of Spraying on Transpiration.—Duggar and Bonns[1] carried out a series of experiments to test the effect of spraying

[1] Ann. Missouri Bot. Gard., **5**: 153–176. April, 1918.

with Bordeaux mixture on the rate of transpiration. Using potatoes, tomatoes, marguerites, tobacco, and other plants, they found that the film of Bordeaux mixture and of certain other materials of similar physical characteristics, cause an increase in the rate of transpiration. These results have been confirmed by earlier and later experiments of the same and of other investigators. The experiments of Duggar and Bonns show further that, without exception, with plants of the type named above, the increase in the rate of transpiration occurred mainly, if not entirely, during the night.

Advantage of Transpiration.—It might seem, at first thought, that the loss of water by transpiration is a disadvantage to plants. Of course this would be the case were it not possible for the roots to take in water as fast as it is lost. When this is not possible, transpiration becomes a real source of danger to the plant. Indirectly, however, transpiration performs a great service, for it aids in, and is probably one of the chief causes of, the ascent of liquids taken in from the soil. However, contrary to a long accepted idea, recent studies[1] seem to indicate that absorption of nutrients is little affected by the rate of transpiration. For example, a glass bell-jar was placed over a pan of growing seedlings. The air under the bell-jar soon became saturated, thus largely or wholly retarding transpiration. Measurements showed that the plants absorbed the nutrients just as rapidly under such conditions as when they were transpiring the maximum amount of water vapor.

Transpiration from Stems.—Water is also given off from stems, especially from young stems before a corky layer has replaced the epidermis (*Cf.* p. 262). Stem transpiration is both cuticular and stomatal. Special structures called *lenticels* (described on page 264) develop underneath the stomata of stem epidermis.

The manner in which transpiration may facilitate the passage of liquids through the stem is discussed in the following chapter.

[1] Breazeale, James F. Nutrition of plants considered as an electrical phenomenon. Jour. Agr. Res., **24**: 41–54. 7 Ap. 1923.

CHAPTER V

TRANSPORTATION OF LIQUIDS

Transpiration Current.—We have seen that plants are continually losing water by transpiration, chiefly from the leaves, and that the supply is renewed by absorption by the roots. The wilting of plants does not indicate that the supply of water has ceased, but that water is being lost by transpiration more rapidly than it is being supplied. Since the intake of water is by the roots, it is clear that there must be a continuous passing of water through the stem from roots to leaves. This is called the *transpiration current.* In fact, while the stem and its branches serve to hold the leaves up to the air and light, the transportation of *sap* (water and the various substances dissolved in it) to and from the roots and leaves is one of their chief functions. In order to understand how this is accomplished we must first understand the structure of stems.

Path of the Transpiration Current.—There are, roughly speaking, three main regions of a woody stem, namely, bark, wood, and pith. That sap does not pass through the pith is evident from the fact that the process goes on equally well in older stems, such as tree-trunks, where the pith has been obliterated, and also from the fact that the current is not interfered with when the pith is artificially severed. That the passage upward from roots to leaves is not through the bark may be demonstrated by *girdling* a woody stem, that is, by removing a ring of bark all the way around the stem, down to the wood. When this is done the leaves continue fresh and turgid throughout the season so long as ample water is supplied to the roots. We infer, therefore, that sap rises in the woody part of a stem.

This inference may be verified by immersing the cut ends of various stems or branches in water colored with eosin (red ink will do) or fuchsin. Stems of a lily, a corn seedling, asparagus, bean or castor-oil seedlings, celery, and parsnip are suitable.

The experiment will work more rapidly if the plant material is fresh, and if some of the leaves remain attached to the stems. After the stems have remained in the colored liquid for a few hours (over night if more convenient) they should be removed, their surfaces rinsed, and a half inch or so cut off from the end that was immersed. It will be seen that the colored liquid has

FIG. 43.—Indian corn. Cross-section of stem, showing the irregular arrangement of the fibro-vascular bundles in the parenchyma. Cf. Fig. 44.

risen in the stems, but that it has not "soaked" up through all parts of the tissue, but has followed clearly defined channels, the cut ends of which appear colored in the cross-sectional view of the stem. Moreover, it is easy to classify the stems into two groups according to the arrangement of the channels through which the colored liquid rose.

Monocotyledonous Stem Structure.—In the lily, corn seedling, and asparagus the ends of the channels or *vascular bundles* are

found to be irregularly distributed throughout the cross-section (Fig. 43). They are imbedded in the *fundamental tissue* or *parenchyma*, and are rather more numerous near the outer *rind* than near the center. Such a type of stem structure is called *monocotyledonous*,[1] because it is typical of those plants which have only one seed-leaf or *cotyledon*.

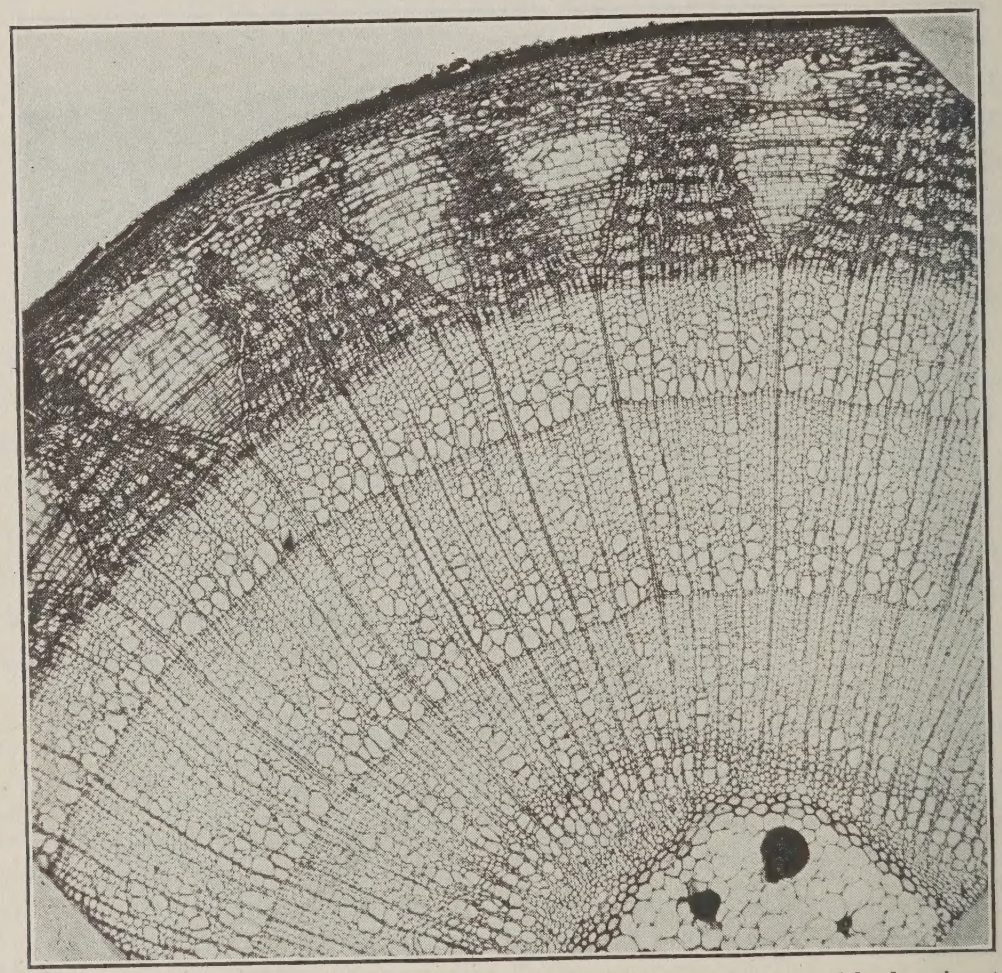


FIG. 44.—Linden (*Tilia* sp.). Cross-section of a stem, 3 years old, showing the cylindrical arrangement of the vascular tissue in the layers of the wood surrounding the central pith. Cf. Fig. 43.

Dicotyledonous Stem Structure.—In the bean or castor-oil seedlings, celery, and parsnip, the vascular tissue is seen to be

[1] The monocotyledonous type of stem was originally called *endogenous*, because it was believed that, in the growth of the stem, new vascular bundles formed only in the central part of the stem, within the region occupied by the older bundles. This conception is now known to be erroneous and the term endogenous, as applied to stem anatomy, is gradually falling into disuse.

confined to a well marked cylinder, imbedded in the fundamental tissue just under the epidermis, and enclosing a solid cylinder of central tissue, the *medulla* or *pith* (Fig. 44). In very young stems the individual bundles appear in the circle, but in older stems the vascular tissue forms a continuous ring. This type of stem anatomy is called *dicotyledonous,* since it is found only in those plants whose seeds have two cotyledons. During growth, stems of this type may increase in thickness by the formation of new woody tissue outside of wood formed during the preceding growing season; for this reason they have been called *exogenous* stems, or *exogens.* The term dicotyledonous, uniform with monocotyledonous, is gradually supplanting the term exogenous. The fundamental tissue between the vascular bundles constitutes the primary *pith rays* or *medullary rays.*

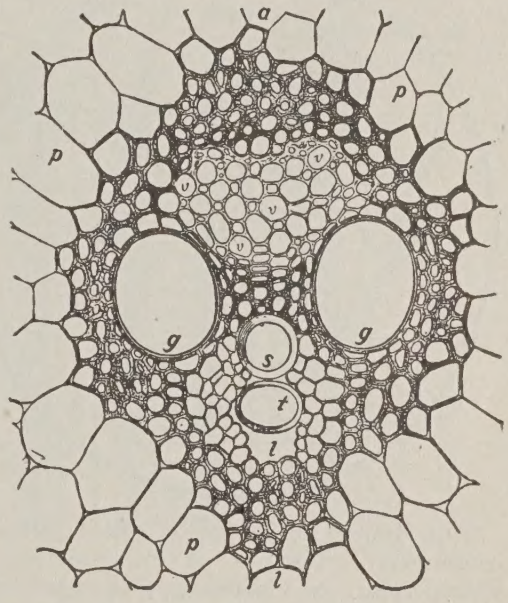


FIG. 45.—Cross-section of a closed fibro-vascular bundle of the stem of Indian Corn. *g,* pitted ducts; *s,* spirally thickened duct; *t,* isolated ring of an annular duct; *v,* sieve tubes of the phloem; *p,* fundamental tissue; *l,* air space resulting from rupture of the cells due to growth. (After Sachs.)

Structure of Vascular Bundles. 1. *Monocotyledonous Bundle.* When a thin cross-section of a vascular bundle of the monocotyledonous type (*e.g.* corn) is examined under the microscope it seems to be composed of a number of elements with a uniformly characteristic arrangement, as illustrated in figure 45. There are usually two large conspicuous rings (g) which are the cross-sections of two large tubes or vessels, whose walls, as seen in longitudinal or surface view, are *pitted.* Between these two vessels lie smaller pitted vessels of wood (*xylem*). Radially from the latter, toward the rind, is a group of tubes with cross-walls perforated like a sieve and therefore called *sieve-tubes;* these with their *companion cells,* constitute the *phloem,* while on the inner side of the smaller pitted vessels are two conspicuous vessels, one with *spiral* and the other with *annular* (or ring-like) thickening of the walls. These constitute the *protoxylem.* These elements are surrounded

by hard walled *sclerenchyma*, and outside of all is the fundamental tissue. Since a bundle of this type is not capable of further development it is called a *closed* bundle. Since the xylem and phloem are side-by-side on the same radius, this type of bundle is also called *collateral*.

2. *Dicotyledonous Bundle.*—In contrast to the monocotyledonous bundle we may choose the bundle of the castor-oil plant (Fig. 46). The surface layer of cells of the stem is the *epidermis*, underneath which is the *cortex*, many cells in thickness; in the center is the *pith*. The cylinder of vascular bundles lies between the cortex and pith. The inner, pointed (when seen in cross sections) end of the bundle is composed of some vessels whose walls are thickened spirally (as seen best in a longitudinal view, Fig. 47), and some whose walls are pitted. These elements constitute the *primary xylem*, or woody portion of the bundle. The opposite side of the bundle, with the *sieve-tubes* and *bast fibers*, is the *phloem*. Between the xylem and the phloem is a layer of several very thin-walled cells, the *cambium*. The cambium is embryonic tissue, and by cell-division it forms new xylem elements on the inside, and new phloem elements on the outside. When cambium is found between the bundles it is called *interfascicular cambium*. Since xylem and ploem may be indefinitely increased by the cell-divisions of the cambium this type is called an *open bundle*.

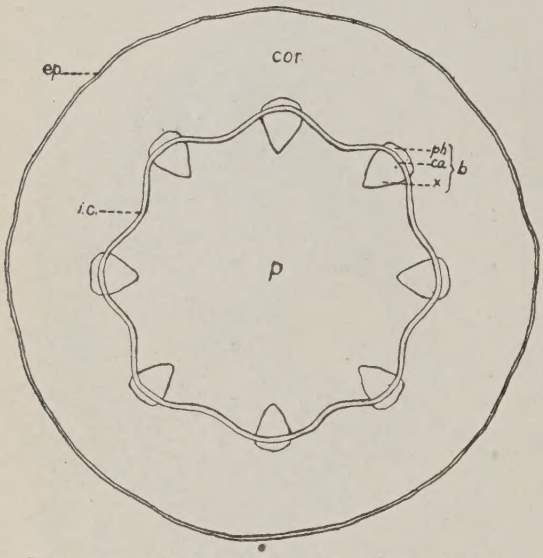


FIG. 46.—The castor-oil plant (*Ricinus communis*). Portion of cross-section of young stem. *co*, Cortex; *p*, pith or medulla; *e*, epidermis; *ph*, phloem; *ca*, cambium; *x*, xylem. The last three elements compose the fibro-vascular bundle, the cambium being continuous from bundle to bundle; the portion between the bundles is called interfascicular cambium.

It has generally been considered (until recently) that mineral nutrients absorbed from the soil were carried upward in solution in the water of the transpiration current, passing through the xylem. But since water and substances dissolved in it pass

through osmotic membranes independently of each other it does not follow that the mineral nutrients must necessarily pass upward with the water. In fact, recent experiments by Muenscher[1] and others have shown that there is no direct relation between the absorption of water and of salts from the soil. This is what would be expected if, as is probable, the upward current was partly by mass movement through open tubes and partly by diffusion through osmotic membranes.

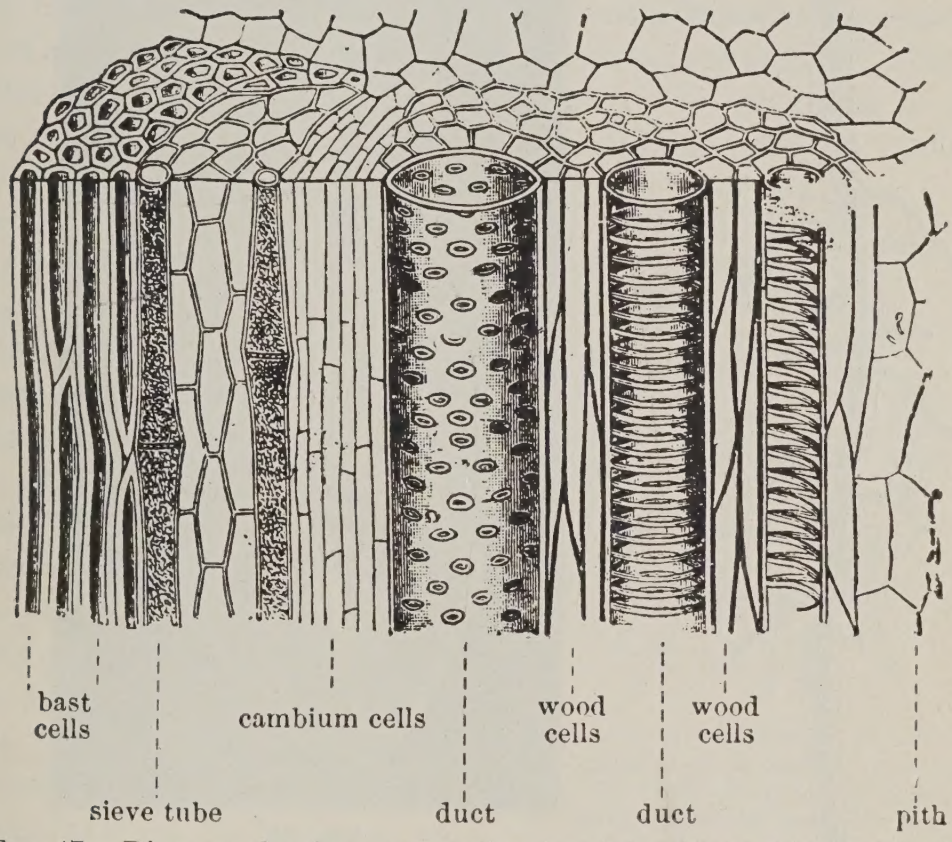


FIG. 47.—Diagram showing cross-sectional and longitudinal sectional views of vascular bundle of a stem of the type of the sunflower (*Helianthus*). (From Peabody and Hunt.)

The question of the upward path of mineral nutrients was investigated by Curtis by girdling branches of peach, cherry, privet, and lilac. As soon as the branches were girdled, sodium nitrate was added to the soil. The experiments showed that girdling hindered the movement of nitrogen and nutrients above the zone of girdling. Curtis concludes that (if the xylem was not injured by the girdling) the ringing experiments offer strong evi-

[1] Muenscher, W. C. The effect of transpiration on the absorption of salts by plants. Am. Jour. Bot., **9**: 311–329. 1922.

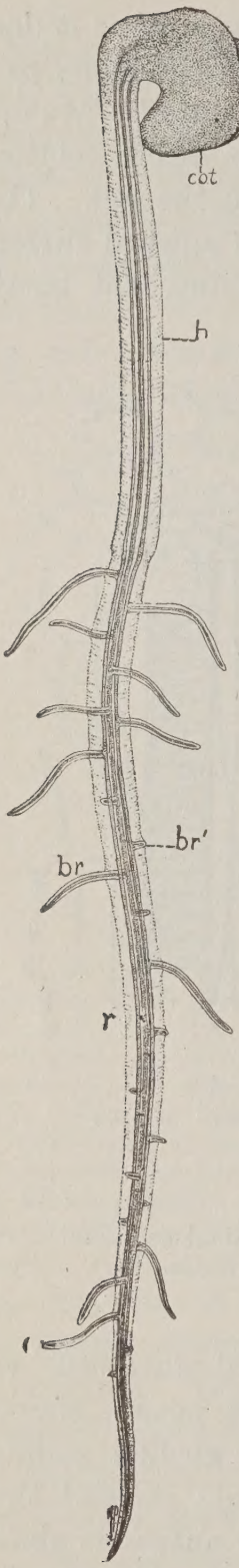


FIG. 48.

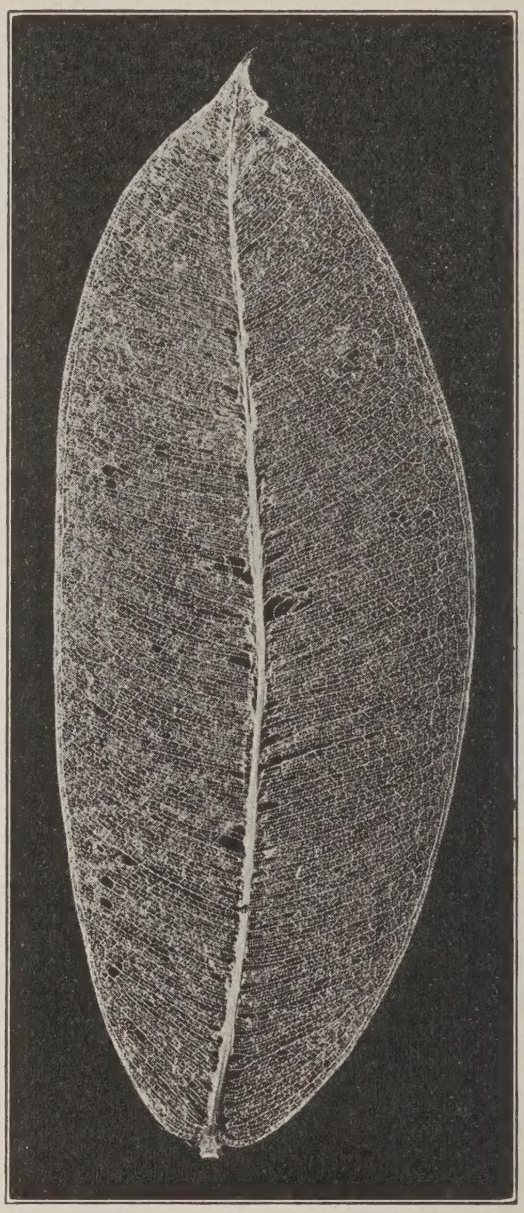


FIG. 49.

FIG. 48.—White lupine (*Lupinus albus*). Made semi-transparent by being placed for several hours in a weak aqueous solution of potassium hydroxide. After this treatment the fibro-vascular system may be clearly seen (through the surrounding tissues) by transmitted light. *cot*, cotyledons; *h*, hypocotyl; *r*, main root; *br*, *br*^{1}, branch roots of different ages. Note the endogenous origin of the branch roots.

FIG. 49.—The system of veins in a leaf of the common rubber-plant (*Ficus elastica*). The veins are connected with the root by means of the vascular bundles extending through the stem and roots.

dence that nutrients are carried chiefly in the phloem. Dixon, however, has presented "cogent evidence" that organic substances are transported, both upward and downward, chiefly through the tracheae of the wood.[1]

Relation of Vascular Bundles to Roots and Leaves.—From what has been said in the preceding paragraphs and chapters, it will now be recognized that the root-hairs and leaf-veins are, in reality, the opposite terminals of the vascular system of the stem. The bundles extend down into the roots, and though they cease to exist as structural elements before the root-tip is reached, there is cellular continuity from the root-hairs to the beginning of the bundles. At their opposite extremities they extend out through the petioles to the blades of the leaves, where they are known as the leaf-veins, here, too, somewhat modified (Figs. 48 and 49).

In roots, the xylem and phloem alternate so that any given radius passes through either xylem or phloem, but not through both, forming a *radial bundle* (Fig. 50). In the leaf the vascular elements are arranged in three groups, as follows: 1. On the side nearest the lower surface of the leaf are elongated, thin-walled cells, with a thin lining-layer of protoplasm, and with the cross walls perforated, forming the *sieve-tubes;* 2. Above the sieve-tubes a group of cells and tubes formed by the fusion of two or more cells end to end. The cells are called *tracheids,* and the tracheal tubes, *ducts;* 3. Enclosing these elements is the *bundle-sheath,* composed of elongate living cells. Liquids pass *into* the leaf from the stem through the ducts and tracheids, and *out of* the leaf into the stem through the sieve-tubes and bundle sheath (Fig. 51).

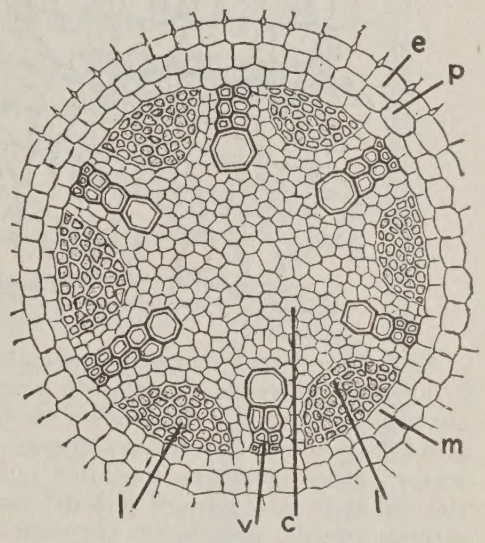


FIG. 50.—Cross-section of the central cylinder of a root of a dicotyledon (*Aranthe elongata*) to illustrate the radial type of vascular bundle. *e*, inner layer of cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, phloem bundles; *v*, xylem bundles; *c*, pith and medullary rays. (From Goodale, after Van Tieghem.)

[1] Curtis, Otis F. The effect of ringing a stem on the upward transfer of nitrogen and ash constituents. Am. Jour. Bot. **10**: 361–382. 1923.

Dixon, and Dixon and Ball. Notes Bot. Sch. Trinity College, Dublin **3**: 207, 234. 1923.

The Ascent of Sap.—To explain the ascent of sap, especially in very tall trees and vines, has been one of the most baffling problems of plant physiology, and no wholly satisfactory or adequate theory has yet been proposed. It seems certain, however, that a number of factors are involved, among which are: 1. So-called "root-pressure;" 2. The so-called "lifting power" of transpiration; 3. The secretion of water in the tissue of leaves.

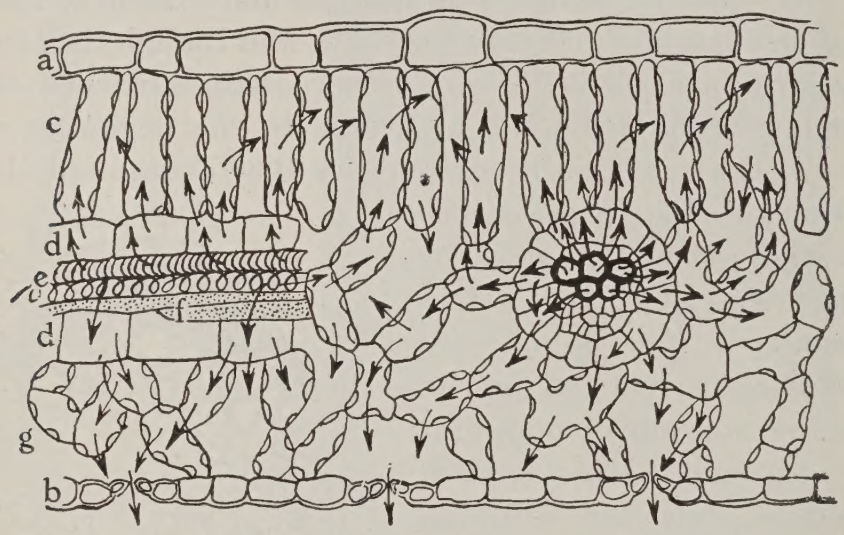


FIG. 51.—Cross-section of a leaf (semi-diagrammatic). *a*, upper epidermis; *b*, lower epidermis; *c*, palisade parenchyma; *d*, bundle sheath (border parenchyma); *e*, vascular elements with spiral and annular ducts and tracheids above and sieve-tubes below; *g*, spongy parenchyma. The arrows show how the water passes from the vascular bundle to the bundle sheath, and thence into the palisade and spongy parenchyma, from which it evaporates into the intercellular spaces, and thence through the stomata to the outer air in transpiration. (After Stevens.)

1. *Demonstration of "Root-pressure."*—If a bean seedling, or other vigorous young plant growing in a flower pot, is cut squarely off two or three inches above the surface of the soil, a drop of sap will soon collect on the cut surface. We say that the stump is "bleeding." Gardeners are familiar with the phenomenon, and are careful not to prune in the season when the sap is rising vigorously, as the bleeding may be copious enough to weaken the plant. The bleeding is caused by the *exudation* or secretion of water from the uninjured cells at and near the cut surface. *Guttation*, or the expulsion of water in drops from the leaf-margins of various plants is due to a like cause. As we have seen in a preceding chapter (p. 64), the secretion of water is initiated by the pressure of the cell-sap brought about by osmosis. With

reference to the bleeding of plants this pressure is often referred to as *exudation pressure.* There is, of course, an unbroken chain of osmotic couples from the cut surface to the root-hairs, where the pressure begins as a result of the osmotic absorption of soil water; but most of the sap that appears in bleeding is forced into and up through the tracheids and ducts of the vascular bundles by the osmotic pressure of the adjacent cells. Since the pressure begins in the roots it is commonly referred to as "*root-pressure.*" The fact that there is a very considerable pressure may be demonstrated by a simple device. A pressure gauge, or *manometer* (Fig. 52), is attached by a piece of rubber tubing to the stump of a vigorous geranium, impatiens, or other convenient plant which has just been cut off three or four inches above the surface of the soil; the height to which the mercury rises in the long arm of the gauge is an index of the amount of the exudation pressure. Professor Vines cites an experiment with a stinging nettle in which the mercury was raised to a height of 354 millimeters, which is equivalent to nearly half an atmosphere, or sufficient to support a column of water about 15 feet high. In some plants the exudation pressure has been found sufficient to counterbalance a column of water 36 feet high; in other words, the sap would still exude even if the cut surface were pressed upon by a weight equal to the weight of a column of water of the diameter of the stem and thirty-six feet high.

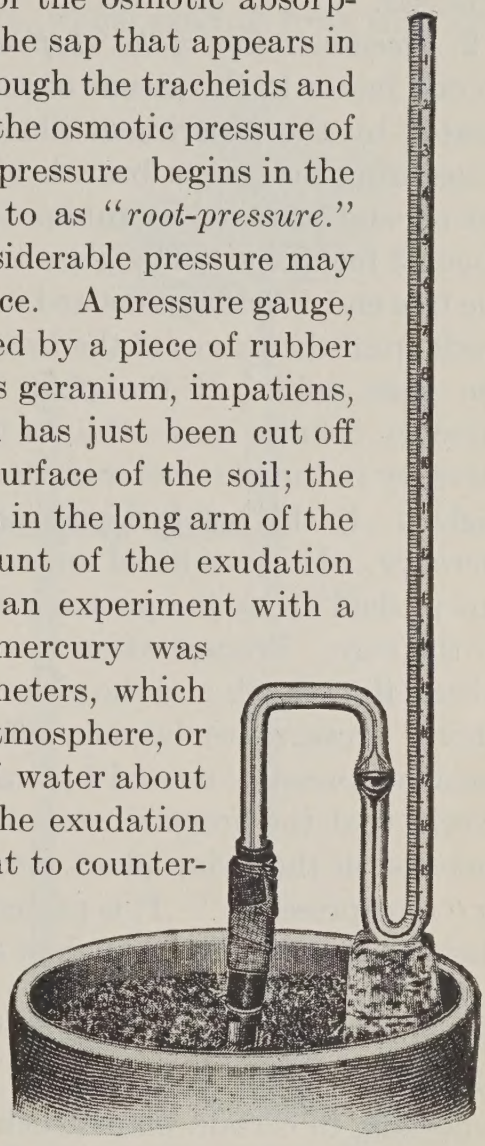


FIG. 52.—Manometer for measuring the pressure caused by the sap exuding from the stump of a stem after the upper portion has been cut off. This was formerly called "root-pressure," but is more correctly called exudation pressure. (After Ganong.)

"Root-pressure" was formerly considered an important factor in causing the ascent of sap; but it has been found by experiment that root-pressure is lowest when the ascent of sap is most vigorous. It has also been demonstrated that there is a negative gas pressure in the vascular system of the stem, which would not

exist if the sap were being forced up by pressure at the roots. For these and other reasons "root-pressure" is not now thought to be as important a factor in the ascent of sap as was formerly believed.

2. *Demonstration of the "Lifting Power" of Transpiration.*—The second factor in the ascent of sap, named above, may be demonstrated by the experiment illustrated in Fig. 53. A vigorously transpiring branch (a branch of a pine tree is recommended) is cut off and fastened by rubber tubing into one end of a glass tube about 3 feet long. The glass tube is then filled with water, and the free end quickly immersed in mercury. As transpiration proceeds from the leaves of the branch, the mercury is seen to rise in the glass tube. If the plant remains in good condition the mercury column may attain a height equal to the height of the mercury in the barometer at the time of the experiment—but not higher. In this last fact is found the explanation of the rise of the mercury. It is not lifted up, as the words "lifting power" imply, but pushed up by the pressure of the atmosphere on the mercury in the cup. Transpiration merely results in a *negative pressure* within the branch and the glass tube, and this permits the atmospheric pressure to become effective. In the living plant the negative pressure caused by transpiration acts in a similar way, except that the pressure caused by the atmosphere in the experiment is, in the living plant, produced by the exudation pressure or "root-pressure." It is probable that capillarity in the vascular tissue is also a factor, though of how much importance is not clear.

3. *The Secretion of Water in Leaves.*—It has long been recognized that "root-pressure" and the "lifting power" of transpiration are not sufficient to account for the ascent of sap, especially in certain plants such as very tall trees and vines, and under certain conditions, such as the submergence of aquatic plants, where transpiration cannot, of course, occur. Investigations[1] have shown that the processes of secretion and osmosis in the leaf are important factors in the ascent of sap. The mesophyll cells of the leaves first secrete a solution to the outer surface of the cells, and this solution becomes concentrated by evaporation of the liquid solvent into the intercellular spaces. The con-

[1] See Dixon, H. H. Transpiration and the ascent of sap in plants. London, 1914.

centrated solution then, by osmotic action, causes more water to be withdrawn from the interior of the cells, and these, in turn, are replenished from the vascular bundles. On account of the *tensile strength* of the water column, which extends from the veins down through the ducts of the stem to the roots, the water is raised as rapidly as it is transpired by the leaves.

On the basis of the combined action of secretion, osmosis, and "root-pressure," we may account for the ascent of sap in submerged aquatic plants, such as the pondweeds (*Potamogeton*), eel-grass, and others, where transpiration cannot take place. It has been shown experimentally, by Dixon, that a leafy branch can raise water through the vascular bundles, even when submerged. The apparatus is set up as shown in Fig. 54. The leafy branch, immersed in water in an inverted glass bell-jar, has the cut end of the stem in a solution of eosin, or red ink. Under these conditions, only osmosis (between the mesophyll cells of the leaves and the intercellular spaces) and secretion can operate to withdraw water from the bundles, and yet the eosin rises through the vascular bundles of the stem and into the leaves.

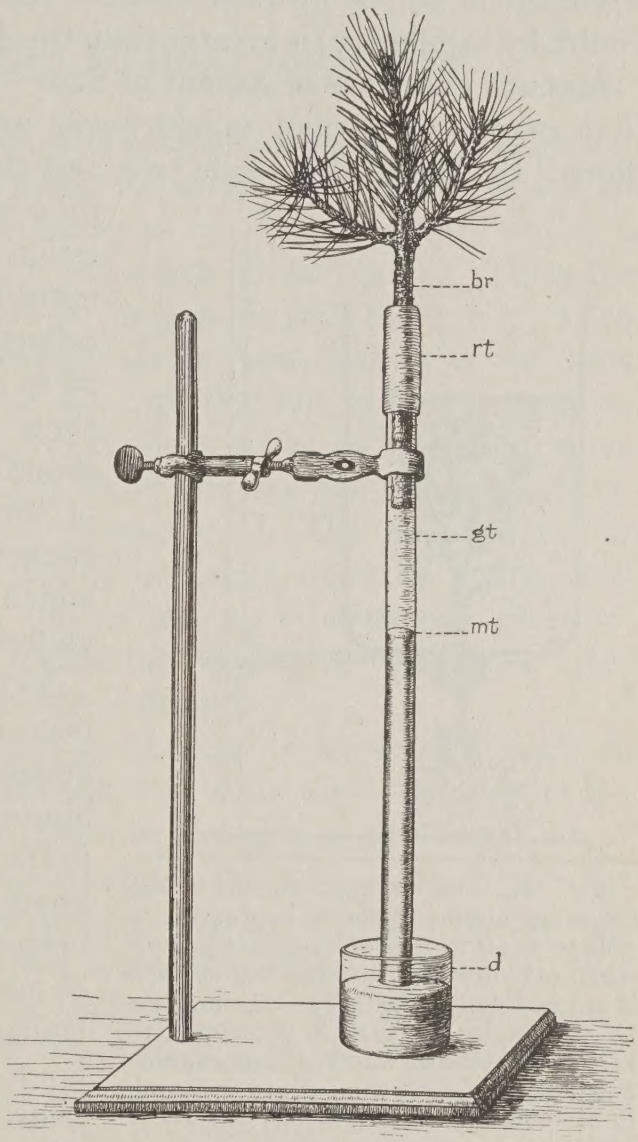


FIG. 53.—Experiment to illustrate the so-called "lifting power" of transpiration. *d*, dish of mercury; *mt*, surface of mercury column that has risen in the glass tube, *gt*; *rt*, rubber tube; *br*. branch of a pine tree, whose leaves are transpiring.

In tall trees and vines the water column in the tracheids is subject to a considerable downward pull of gravity (its own weight), and the upward pull caused by the physiological processes in the leaves, and yet it does not separate, because of its tensile strength; it moves upward because the upward pull (aided, no doubt, by capillarity) is greater than the downward pull of gravity.

Amount and Rate of Ascent of Sap.—Most people understand that maple syrup and maple sugar are obtained by "boiling down" the sap of the maple tree, but the amount of sap yielded by a single tree will be a revelation to many. It is not unusual in a "sugar bush" to collect from one tree as much as 25 to 30 quarts daily for two or three weeks. Sugar is also sometimes made from the sap of the black birch, and an instance is on record of a tree which yielded almost 1900 gallons of sap in about 30 days.

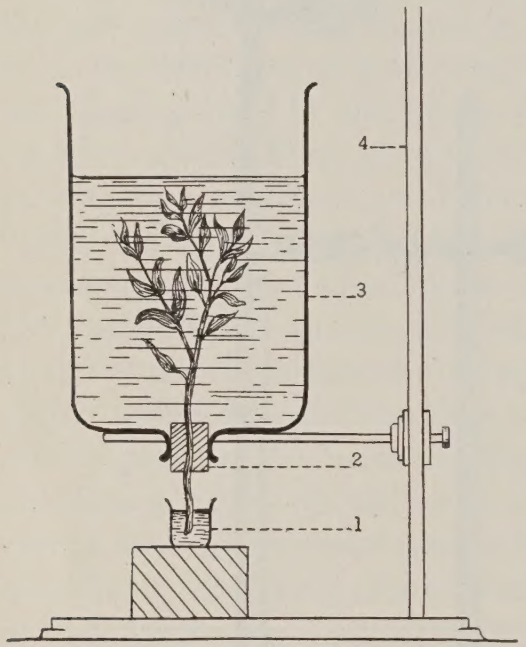


FIG. 54.—Experiment to show that secretory action in the cells of a leaf is able to cause the rise of liquid in a branch, when evaporation from the leaf surfaces is impossible. 1, Beaker containing solution of eosin; 2, cork; 3, inverted glass bell-jar containing water; 4, iron support. In this experiment the eosin rose rapidly in the branch. (Modified from H. H. Dixon.)

As to the rate of ascent, it has been found that when a white flowered Iris was watered with a blue solution the color appeared in the white petals within 10–15 hours. The sap in a willow has been observed to rise at the rate of nearly three feet an hour, in Indian corn over 14 inches an hour, in a sunflower 25 inches an hour. In the tobacco plant (*Nicotiana*), which transpires copiously and wilts readily, the rate is nearly four feet an hour. Gaye[1] is authority for the statement that in one of the water-lianas (rope-like vines) of the American tropics, a pint of water passes a given point in the stem in less than a minute, which is at the rate of 60 pints an hour, or 90 gallons in a day of twelve hours. This, of course, is an extreme instance.

[1] The data in the two paragraphs under the above caption are from "The Great World's Farm," by Selina Gaye. London, 1894. pp. 108–109.

CHAPTER VI

THE STRUGGLE AGAINST DROUGHT

Supply and Demand.—From a comparison of the water requirements of plants and the amount of precipitation it may be shown that the quantity of water falling as rain in any locality during a given period is not equal to the needs of the plants. Thus, for example, the wettest month in England is said to be July, when the precipitation averages only about three inches, or 300 tons per acre; but the grass on an acre of pasture land transpires about 106 tons of water in twenty-four hours, or more than three thousand tons a month—ten times the amount of precipitation. Evidently two things are necessary: 1. The conservation of water in the soil so that it may be drawn upon by plants continuously, and especially during periods of slack precipitation; 2. Arrangements by the plants for protecting themselves from injury or death during periods of drought.

Definition of Drought.—It is common to think of drought in terms of rainfall or precipitation, but, from the standpoint of the plant or the crop, drought must be thought of as a condition of the soil with reference to moisture content. Rotmistrov[1] has defined drought as "a temporary scarcity of water in the soil, affecting plants and holding back the normal course of their life processes;" but we know that not all drought is "temporary," for in certain portions of the Sahara and the frozen tundras, and other desert regions the scarcity of water in sufficient amount to allow of any growth of plants is perennial.

Distribution of Soil Moisture.—Water percolates through the soil in all directions, chiefly by capillary action. It is often stated that water will in this way rise, from depths inaccessible

[1] Rotmistrov, V. G. The nature of drought. (Eng. translation from the Russian.) Odessa, 1913. This monograph has been freely drawn upon for the above paragraphs. The author states (p. 12) that it is based on "several thousand sets of statistics" accumulated during 15 years of investigation at the Odessa Experiment Field.

to roots, up to the root-inhabited layers; but there seem to be grave doubts as to the reality of this, for laboratory experiments have failed to demonstrate that water can rise in this way more than a few inches, while the vertical distance from the region of roots down to that of permanent water supply is usually a matter of several feet. It is stated by Rotmistrov that, in the arid regions of south Russia, water percolating beyond a depth of 40 to 50 cm. (15–20 inches), if not absorbed by the roots, sinks down into the deeper layers of soil at the rate of about 7 feet a year.

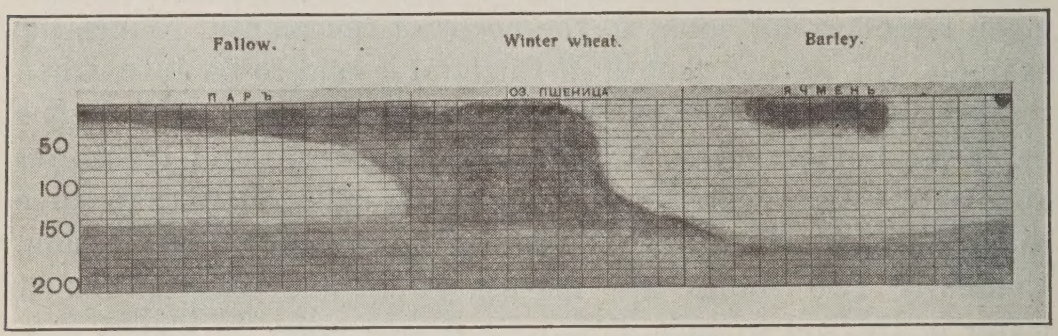


Fig. 55.—Diagram showing state of soil humidity during a three years rotation of fallow, followed in succession by winter wheat and barley. The three soil conditions shown from left to right represent the conditions during three successive seasons (not on three adjacent fields). The humid layer gets so deep during the fallow that, when winter wheat is sown, its roots can develop to full normal length, for they do not meet an intermediate dry layer in the whole of their extent. Such a large reserve of water in the soil after clean bare fallow assures the winter crop even in a dry season. The winter wheat uses all the useful water in a soil layer 120 cm. deep, but below that there is still a reserve that sinks gradually to the level of the permanent humid lower layer by the following winter (as shown at the right of the diagram). In the following spring barley is sown. (Diagram and part of legend after Rotmistrov.)

With reference to moisture content three regions of the soil were recognized by Rotmistrov in Russia, as follows (Fig. 55):

1. The periodically humid layer.
2. The intermediate dry layer.
3. The permanently humid layer.

1. *The periodically humid layer* varies in moisture content with the season and the amount of precipitation. It is the *root-inhabited layer*, and varies in depth from about 2½ feet for potatoes and other crops, to as much as 4½ feet for sunflowers and other plants. In the case of most cereals the depth is about 3½ feet. Water accumulates in this layer during autumn, winter,

and spring, and this reserve, or as much of it as can be utilized by plants (the *serviceable water*), is practically all used up by the vegetation and surface evaporation between spring and the end of summer—or while the crop is maturing. If a field is left fallow this layer retains its available or serviceable water throughout the year (Fig. 55).

2. *The permanently humid layer* begins at a depth of 4–5 feet, depending on the nature of the soil and the climate of the region, and extends downward to the *water table*[1] or upper surface of the ground water.

3. The *intermediate dry layer* contains only about 10% of moisture, not available to plants. This layer is periodically moistened from the humid layers above and below it.

Cultural Methods to Counteract Drought.—When rotation is not practiced, a succession of cereal crops, for example, exhausts

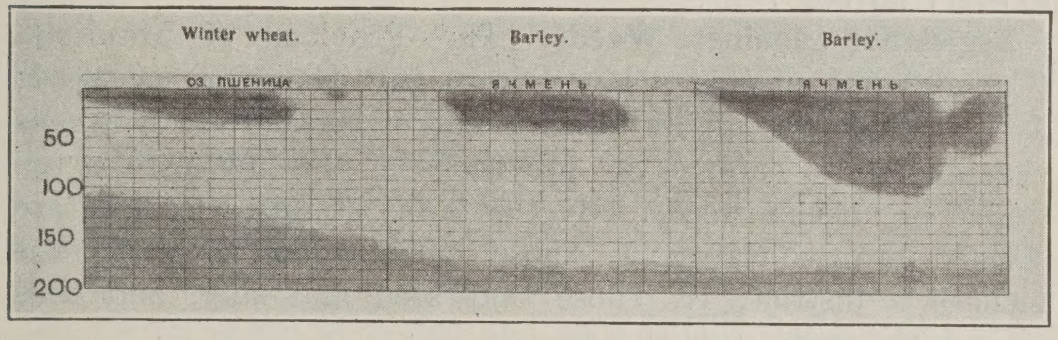


FIG. 56.—Diagram showing how uninterrupted culture of cereals diminishes the soil humidity and thus, in effect, impoverishes the fertility of the soil. Every year the farmer finds himself threatened with drought. (After Rotmistrov.)

the water from the lower portion of the layer inhabited by their roots (Fig. 56). The dissolving of mineral salts is thus diminished, which amounts to impoverishment of the soil. From consideration of this fact we can appreciate the value of a crop rotation planned with the idea of an alternation of long-rooted plants with short-rooted, of densely rooted with sparsely rooted; such a succession, for example, as winter wheat or rye (long-rooted)—potatoes (short-rooted)—barley or oats (long-rooted)—flax (short, sparsely-rooted)—rye, which Rotmistrov recommends as almost ideal for the black earth of the steppes of southern Russia.

[1] The term *water table* applies to the upper limit of that portion of the soil completely saturated with water.

Weeds and Drought.—The presence of weeds in early spring before the crop is planted also conduces to drought, for they may absorb a large portion of the available water in the root-inhabited layer. Similarly, autumn weeds exhaust the upper soil-layer of the water which falls after the crop is harvested. "A big weed takes a barrel of water out of the soil. A crop of wheat takes 900 tons of water per acre; so does a crop of weeds" (Manitoba Dep. Agr. Extension Bull. 30). The bitterest enemy of field culture and the best friend of drought are the weeds, and the farmer or gardener should endeavor to prevent a single drop of water being wasted on the growth of weeds. "The extirpation of weeds on the whole space of the land possession," says Rotmistrov, "and a correct rotation of crops with a persistent alternation of cereal grasses and thorough ploughed plants, are measures of fighting against drought which are accessible to every farmer . . ."

Legislation against Weeds.—The Province of Manitoba (Canada) has enacted a law, known as "The Noxious Weeds Act," establishing in its Department of Agriculture a Weeds Commission to enforce the provisions of the law against the spread of noxious weeds. By the terms of this act weeds are divided into two classes: I. Those that blow and sow, and thus menace a district; II. Those that seed and stay, and thus menace the farm.

The law provides that all occupants or owners of land must destroy all barberry bushes (Cf. p. 524 of this book), shall cut down or otherwise destroy all noxious weeds of Class I growing on their land, and weeds of Classes I and II "on every road or highway immediately adjoining such land to a distance or extent of one half the width of such road or highway nearest to such land as often as may be necessary to prevent the ripening and scattering of the seeds of noxious weeds of such classes." Railway companies must also prevent the ripening and scattering of these seeds along their right of way. Threshers must clean their threshing machines, wagons, and entire outfit so as not to carry weed seeds to the next place of threshing, and a copy of this section of the law must be affixed to every threshing machine. If the inspectors find a crop badly infested with weeds they are authorized to cut down as much as three acres of the crop in

any one quarter section (one half mile square) of land without notice, and, on notice to the proper persons, a larger area of crop may be cut down to prevent the ripening and spread of the weed seeds. If any parcel of land is found to be infested with noxious weeds "to a detrimental extent" the owner may be forbidden to rent such land. Heavy penalties are provided for failure to keep these laws, and if a tenant suffers any loss of crops due to weeds the owner is liable not only for the penalties for violating the law, but must in addition reimburse the tenant for the amount of his loss.

It is further unlawful to sell seed of any agricultural crop or any feed products containing seeds of noxious weeds in excess of the regulations prescribed under any statute of the Dominion of Canada. It is unlawful to sell hay or other fodder containing the ripe seeds of couch or quack grass, unless the purchaser is informed in advance that the hay contains such seeds. It is further unlawful to place weed seeds on any public road, railway, highway, street, or lane. This law is striking evidence of the real menace of weeds, and of the recognition of this fact by at least one organized government.

Fighting Weeds in Rice Fields.—In the rice-growing regions of California the fields were formerly flooded and drained alternately until the rice was sprouted. This favored the growth of weed seeds as well as of rice, and, as is usually the case, the weeds easily got the better of the crop plants. But rice seed will germinate under water while the weed seeds will not. As soon as the growers realized this, they adopted the method of flooding their fields to a depth of 4–8 inches after planting, allowing the water to remain until the rice had germinated. By this practice the rice gets the better of the weeds.

According to Beech,[1] the farmers of Szechuan (1000 miles west from the coast of China) have the responsibility of feeding a nation of 60 million people on an area of less than one half that of the State of Texas, and which must be self-supporting. Systems of irrigation make these farmers independent of rain (as they must be if actual famine is to be avoided). These Chinese certainly appreciate the menace of weeds. "The roily water makes the hoeing of his rice field impossible; so he does not hoe it;

[1] *Nat. Geog. Mag., Nov.*, 1920.

he toes it. With bare foot he feels about the plant with his toes, and if he finds a weed, he toes it out; then presses the dirt firmly in place again. With his right foot he toes two rows, with his left foot he toes two rows, and thus he toes four rows as he goes. That's the way he hoes."

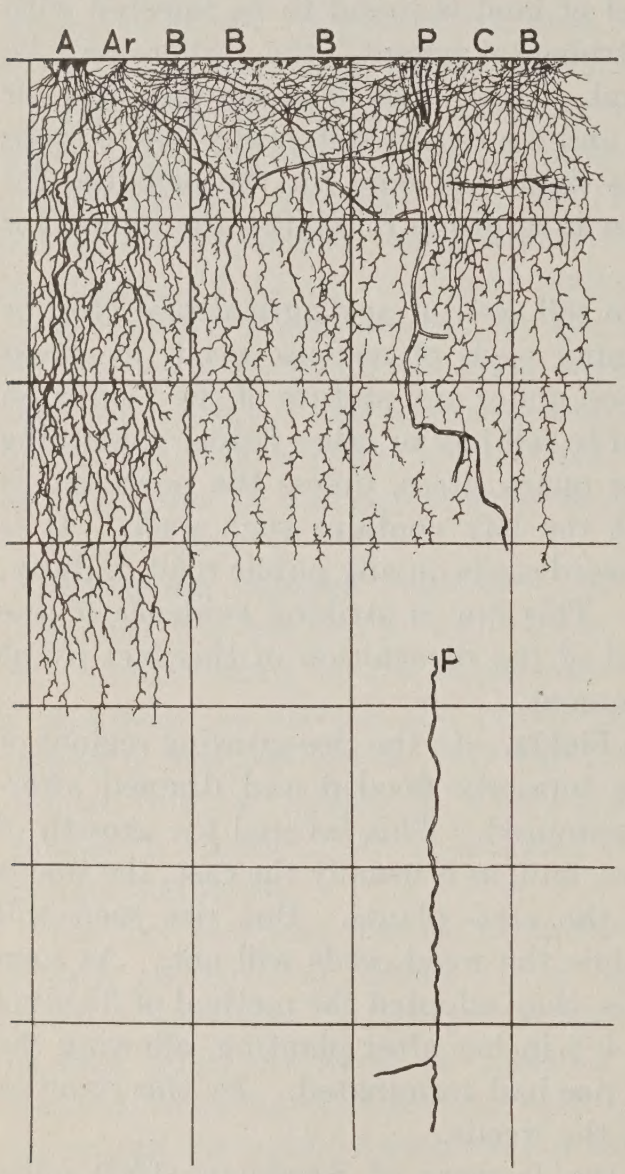


FIG. 57.—Section through a square meter of soil, showing the root-distribution of certain dominant and sub-dominant species of the plains region of the United States. Each different letter indicates a different species of plant, some shallow- and some deep-rooted. P indicates the root system of *Psoralea tenuiflora*. (After Weaver.)

Root Competition for Moisture.—The extent to which the soil may be occupied (almost completely) by the roots of plants is strikingly illustrated in Fig. 57, which shows accurately the position of the roots and the conditions of competition, as shown in a section or bisect of a meter-quadrat showing dominant and sub-dominant species of the plains region of the United States.

The apparent infertility of soil around trees has long been noted, and various theories have been advanced to account for it. One theory attributed the trouble to the diminished light and air brought about by the shade of the trees, but this did not account for the fact that the apparent "infertility" often extends beyond the limits of the shade, and exists also on the south and comparatively unshaded side of

the tree. Moreover, at the Woburn (England) Experimental Fruit Farm, Pickering, by erecting canvas, simulated and even exaggerated the shade of trees, while other conditions remained the same. The crop under the canvas was as large as that in the unshaded portion of the field. Evidently shade is not an adequate explanation.

It has also been suggested that trees deprive the surrounding crop-plants of soluble mineral nutrients, but an actual chemical analysis did not show that the soil under the trees was any poorer in plant nutrients than soil 20–30 yards away.

Recent experiments in South Africa by Williams[1] indicate that the deleterious effect of the trees is due chiefly, if not solely, to their extraction of moisture from the soil. For example, when pumpkins were grown so that their roots competed with the roots of near-by trees, their broad and copiously transpiring leaves would wilt on hot afternoons in the early part of the season, but recover their turgor in the cool evening when transpiration was retarded. Later in the season the wilt became permanent and the plants nearest the trees died, although the plants in the center of the same field, not influenced by the trees, did well and a good crop resulted.

When the soil under the trees and at distances of as much as 50 yards away was tested for capillary water, the latter soil was found to have twice as much capillary water as the soil under the trees.

Under certain conditions crop plants suffer when their roots come into competition with those of trees. Thus Hall, the former director of the Rothamsted Experimental Station, states, in his book on "The Soil," that when meadow grass and vegetable crops are grown under and around newly planted young fruit trees the trees suffer noticeably owing to the fact that the surface plants deplete the soil of its moisture at a critical season for the trees, when they are only imperfectly supplied with water-absorbing roots, and cannot successfully compete with the great mass of fibrous grass-roots. Hall also found that the amount of moisture in the top foot of pasture land was only half that present in the corresponding layer of neighboring uncropped land.

[1] Williams, C. O. Apparent infertility of the soil around trees. Jour. Dept. Agr. Union of So. Africa, **5**: 254–258. Sept., 1922.

Conservation of Soil Moisture.—In addition to cultural methods, vegetation itself is the most important of all agents for the conservation of soil moisture. When water falls as rain, some of it soon evaporates back into the air, some of it sinks into the soil, and some of it runs off in streams, eventually to the ocean. The average amount of rainfall discharged into the sea by all the streams in the world is from one fourth to one fifth of the precipitation. For the United States this has been estimated at about 6500 cubic miles of water annually, or sufficient to cover the entire surface of the country to a depth of over nine feet. The Yukon and the Rhine rivers discharge about one half the rainfall of their valleys, while the Nile discharges only one thirty-seventh.

But more important than the total amount of stream discharge, so far as vegetation is concerned, is the rate of discharge, which, of course, depends on the rate of surface and sub-surface run-off from the watershed to the stream. If this is rapid the soil becomes rapidly dry, and unsuitable to support plant life. Moreover, in the case of rapid run-off, much of the soil is likely to be carried along with the drainage water, and thus the land is impoverished.

Vegetation operates in several ways to retard the run-off, and cause the rain water to be retained in the soil. In the case of forests the dense foliage, by transpiration, by excluding the heat of the sun, and by reducing the wind under the trees, retards evaporation from the surface of the soil. The leaf-mold on the forest floor operates in the same way, serving as a mulch. The mass of roots in the soil helps to form a spongy condition favorable to the retention of the water, and this condition is further aided by humus in the soil, formed by the disintegration of vegetable matter. This results in retarding the surface drainage into the streams and thus in maintaining the water-table of the ground-water, at a higher level. It is probable also that the presence of forests tends somewhat to increase the amount of rainfall.

The great importance of vegetation, and especially forests, in regulating the drainage of the soil, and, to a lesser degree, the amount of precipitation can hardly be overestimated. The destruction of forests, by removing this factor, has resulted in changing a large part of several fertile countries into barren

wastes, for the soil has not only been deprived of its moisture, but has been carried down to the streams and finally deposited in the ocean, leaving only barren slopes where there was formerly a fertile agricultural region. Palestine, Spain, and China are conspicuous examples of regions where this has occurred. Various parts of the United States have been spared this irreparable damage only through the success of the conservation movement.

Periods of Drought.—Periods of drought are sporadic, seasonal, and perennial or permanent. *Sporadic* periods are due to irregularities of the *weather*, and may fall in the spring, midsummer, or autumn.

Seasonal drought is an expression, not of weather, but of climate.[1] In the eastern United States we are most familiar with seasonal drought, for the period of winter, so far as vegetation is concerned, is a *dry*, rather than a cold, season. The groundwater becomes solid (frozen) for a certain depth below the surface, and can therefore not be absorbed by roots.

In other places which have no "winter" (in the sense of a cold season alternating with a warm "summer"), there is a periodic or seasonal alternation of rainy season and dry season. The rainy season of Japan, for example, extends from April to September. In southern California the rainy season comes during the winter months, the summer being a period of rather severe drought. In the llanos of Venezuela the rainy season comes during the summer months, while south of the equator, in the campos of Brazil, the dry season is in summer and the rainy season in winter. *Perennial drought* results in the formation and maintenance of a desert.

Deserts.—The essential thing about a desert is the almost total absence of moisture. It is a widespread error that the chief characteristic of a desert is sand; the fact is that sand is one of the scarcest materials in many deserts. A desert may have very rich soil and yet be a desert solely because of the small amount of moisture. The frozen *tundras* of the polar regions are as true deserts as is the Sahara for, though there is water there, it is

[1] "The term *weather* includes all the atmospheric conditions that an observer may feel or see,—hot or cold, clear or cloudy, dry or wet, windy or calm." (W. M. Davis.) The *average* annual succession of weather changes throughout a series of years constitutes the *climate* of a region.

frozen solid, and is therefore not available for vegetation. The absence of water, except sporadically or in isolated *oases*, results, of necessity, in the absence of vegetation; the absence of vegetation, especially such as furnishes food for grazing animals, results in the absence of the latter, and thus in the absence of men dependent upon grazing animals and crops for their existence. Only a comparatively small portion of the fifty-three million

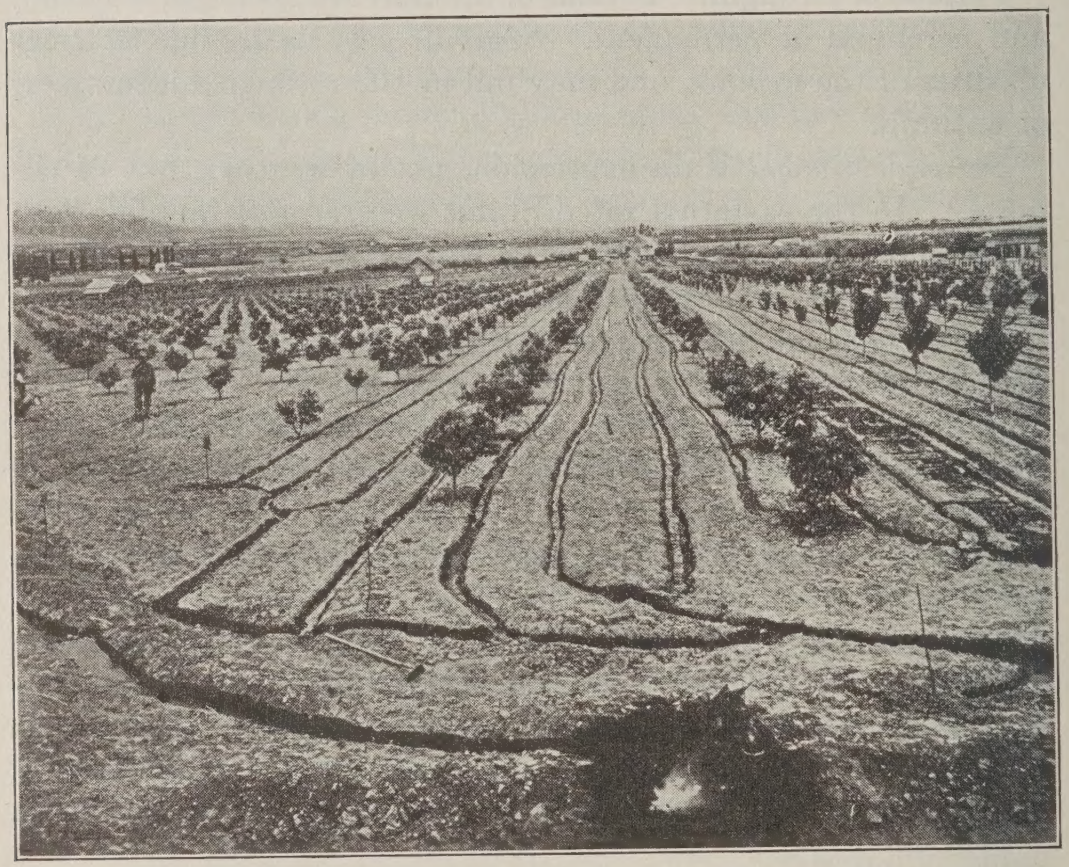


FIG. 58.—Irrigation of a young orchard in the Western United States. (By courtesy of Public Photo Service, Inc.)

square miles of land surface is capable of supporting man and the higher animals. In the United States, for example, fully one half the land area is too feebly productive to support more than a scattered population.[1] Most of Australia is an uninhabitable desert. Various causes may render a region inhospitable for

[1] The total land area of the United States is 1903 million acres, of which only about 47% (approximately 840 million acres) was included in farms in 1915. Only about one half of this land is improved. By irrigation about 40 million acres can be added.

man—too high or too low average temperature, excessive rainfall, absence of soil—but one of the most important controls is rainfall, its total amount and, in particular, its distribution throughout the year. It has been calculated that about one-sixth of North America, Europe, and Asia, and one-third of Africa are too dry to support more than a sparse population. This is true of the United States from about the 100th meridian west to the Sierra Nevada Mountains and Cascade Range. Over an area including parts of Wyoming, Colorado, Arizona, and New Mexico, and the larger part of Nevada and Utah the average annual precipitation is less than 12 inches a year; and in certain portions of Arizona, southern California, and Nevada, less than 5 inches, or quite inadequate to permit the growth of pasture grass in sufficient quantity to support cattle. In addition to the scant precipitation, the humidity of the air in June and July may not rise above 6%; while the thermometer registers 100°–112° F. at midday. Thus, the loss of water by transpiration is most highly favored at the same time that the supply to the roots is reduced to its lowest point. These regions constitute the great American desert, where agriculture is made possible, if at all, only by irrigation and the methods of "dry farming" (Fig. 58).[1]

As an illustration of the opposite extreme of moisture may be mentioned the southern slopes of the Himalaya Mountains, where the average rainfall is 500 inches or about 40 ft. a year, with a record for one exceptional year of 800 inches. Over half of this precipitation occurs during the summer when the monsoon is blowing from over the Indian Ocean, and not infrequently more rain falls in a single day than during an entire year in the eastern United States. Campbell has cited the remarkable rainfall in the Hawaiian Islands, which have a very heavy precipitation on the northeast or windward side, but a very light one on the southwest or leeward side. The contrast is specially marked on Kauai, in the central part of which is Mount Waialeale. Here the average annual rainfall for five years (1912–1916) was

[1] The explanation of this arid condition lies, of course, in the fact that the moisture laden air, carried by the west winds, is cooled as it rises over the high plateau and mountains parallel to the Pacific coast, and therefore parts with its moisture on the west slopes, leaving the great interior region east of the plateau in a desert or semi-desert condition.

518 inches (610 inches in 1914) on the windward side, but only 28.8 inches (24.5 inches in 1914) on the leeward side, only 13.5 miles distant in a straight line. The best condition for agriculture is a rainfall of about 35 to 40 inches, evenly distributed throughout the year.

Volumes might be written to show how the distribution of population depends upon the distribution of the food-producing areas of the world, how these are determined primarily by the possibilities of crop production, and that, in turn, by the amount and distribution of rainfall.[1] The importance, not only to plants but to mankind, of the water relation of plants can, therefore, hardly be exaggerated. The present vegetation of the globe may be said to consist of those plants which have successfully solved the problem of securing and conserving water—the problem of existence on "dry" land.

Sporadic Drought.—The occurrence and results of sporadic drought, due to irregularities of the weather, are strikingly illustrated in the Great Plains region of the western United States. This region is a belt about 350–500 miles in width extending across the United States between the 98th and 105th to 113th meridians of longitude. It includes the western half of North and South Dakota, Nebraska, Kansas, Oklahoma, and Texas (including all of the "panhandle"), and the eastern half of Montana, Colorado, Wyoming, and New Mexico—an area of about one-eighth to one-sixth of the total area of the United States (Fig. 59). Throughout the extent of this region the soil is rich, and the climate suitable to habitation, but the mean annual rainfall is only 10–20 inches, and long periods of drought alternate with those of abundant rain. The result of this sporadic drought is graphically described by Newell[2] as follows:

"Year after year the water supply may be ample, the forage plants cover the ground with a rank growth, the herbs multiply, the settlers extend their fields, when almost imperceptibly, the climate becomes less humid, the rain clouds forming day after

[1] Except for the aid of artificial irrigation, crop production is largely limited to regions having an annual rainfall of not less than 30 inches, fairly evenly distributed throughout the twelve months.

[2] Newell, Frederick H. Irrigation on the great plains. *Year Book U. S. Dept. Agr.* **1896**: 167–196. 1897.

day disappear upon the horizon, and weeks lengthen into months without a drop of moisture. The grasses wither, the herds wander wearily over the plain in search of water holes, the crops wilt and languish, yielding not even the seed for another year. Fall and winter come and go with occasional showers which scarcely seem to wet the earth, and the following spring opens with the soil so dry that it is blown about over the windy plains.

This chart shows for the States east of the Rocky Mountains the number of times in the 20-year period, 1895 to 1914, inclusive, that precipitation to the amount of 0.25 inch in 24 hours did not occur for a period of 30 consecutive days or more, for the season March 1 to September 30, inclusive. Lines show the total number of drought periods for the 20 years.

FIG. 59.—Map showing drought frequency during the crop growing season. The lines show the total number of drought periods for the 20 years from 1895 to 1914, inclusive; that is, periods when precipitation to the amount of 0.25 inch in 24 hrs. did not appear for a period of 30 consecutive days or more for the season March 1 to September 30, inclusive. (From Nat. Weather and Crop Bull., 1915.)

Another and perhaps another season of drought occurs, the settlers depart with such of their household furniture as can be drawn away by the enfeebled draught animals, the herds disappear, and this beautiful land, once so fruitful, is now dry and brown, given over to the prairie wolf. Then comes a season of ample rains. The prairie grasses, dormant through several seasons, spring into life, and with these the hopes of new pioneers.

Then recurs the flood of immigration, to be continued until the next long drought. This alternation of feast and famine is in Europe and the East as old as history and bids fair to be repeated upon our great plains unless American ingenuity, patience, and skill shall devise means of successful irrigation."

FIG. 60.—*Ibervillea sonorae*, growing near Torreo, Mexico. More than half of the succulent, turnip-shaped tuber lies above the surface of the soil. These tubers measure 10 inches or more in diameter. (After Coville and MacDougal. Carnegie Inst. Pub. No. 6.)

PROTECTION AGAINST DROUGHT

Water-insurance, or protection against drought, may be accomplished by plants in variety of ways, operating to enable them to *escape*, or to *endure*, or to *evade* the drought.[1]

Escaping Drought.—Plants that have a short growing season, so that they may mature and set seed during a brief period of water supply, may *escape* drought by the brevity of their life cycle. Such ephemeral plants are not uncommon in desert regions. On the west slopes of the Andes, and notably in Peru, a drought of four or five years may be broken by a fall of rain which awakens the dormant seeds of numerous plants. Some of these are able to produce seed before the next period of drought begins. No cultivated plants are of this character.

[1] Following Kearney, Thomas H., and H. L. Shantz. The water economy of dry-land crops. *Year Book U. S. Dept. Agr.* 1911.

Enduring Drought.—Plants that are able to maintain life, or even to grow, flower, and set seed when the soil is so dry that the roots can obtain practically no water are said to *endure* drought. This is accomplished in at least two ways: 1. By the storage of water; 2. By becoming periodically dormant.

1. *Storage of Water.*—In the museum of the New York Botanical Garden there is a root-stem tuber of *Ibervillea sonorae*, a plant of the gourd family that grows in Mexico (Fig. 60). This tuber, when placed on a shelf in the glass case of the museum in February, 1902, looked lifeless enough, resembling a rock much more than a plant; yet in such a severely arid environment the stem continued to send out, each year, its characteristic long, slender, green stem till as late as the summer of 1908, drawing each year on the water stored up in the desert during the intermittent periods of rain.

FIG. 61.—Giant cactus (*Carnegia gigantea* = *Cereus giganteus*), near Tucson, Arizona. The succulent stems serve for the storage of water. (After MacDougal.)

Striking illustrations of water-storage are found among cacti (Fig. 61). In some of them so much water is stored that the natives utilize the plants as a source of drinking water (Fig. 62). The tip of the stem is cut off and the soft pulp inside loosened and stirred with a stick. The water is then squeezed out of the pulp

into the cavity of the stem in sufficient quantity to afford abundant drink for several men. The leafless, branching stems of these plants may reach a height of 50–60 feet, and may weigh as much as one to two tons; from 85–90 per cent of this weight is water. The roots also serve for the storage of water. It is recorded that, in the region of the Tehuacan desert, in southern Mexico, various species of the genus *Opuntia* may be seen growing on the dirt roofs of adobe dwellings, on stone walls, and even in crevices of brick and stone high up on cathedrals and other large buildings.

FIG. 62.—Papago Indian, near Torreo, Mexico, drinking the water which he has squeezed from the tissue of a cactus (*Echinocactus emosyi*), into the cavity formerly occupied by the tissue. (After Coville and MacDougal.)

Weaver studied the root system of *Opuntia camanchica*, a species of cactus common in the grass lands of the plains region. "As is characteristic of cacti in general, the root system consists of two distinct parts—a few vertically descending anchorage and deep absorptive roots, and a much more extensive and shallow absorbing system. An examinaton of figure 63 shows 23 roots which run off in the surface soil, usually at a depth of an inch and seldom deeper than 3 inches, to distances varying from 6 inches to 6 feet . . . The ultimate root endings, whether of the shorter or larger branches, consisted of much-branched and very

delicate brushlike termini, to which the soil clung with great tenacity . . . The deep anchorage and absorbing system of this plant consisted of 4 main roots . . . These extended vertically downward, following a more or less irregular course through hard soil, branching as shown in figure 63, and reaching a maximum depth of 35 inches."

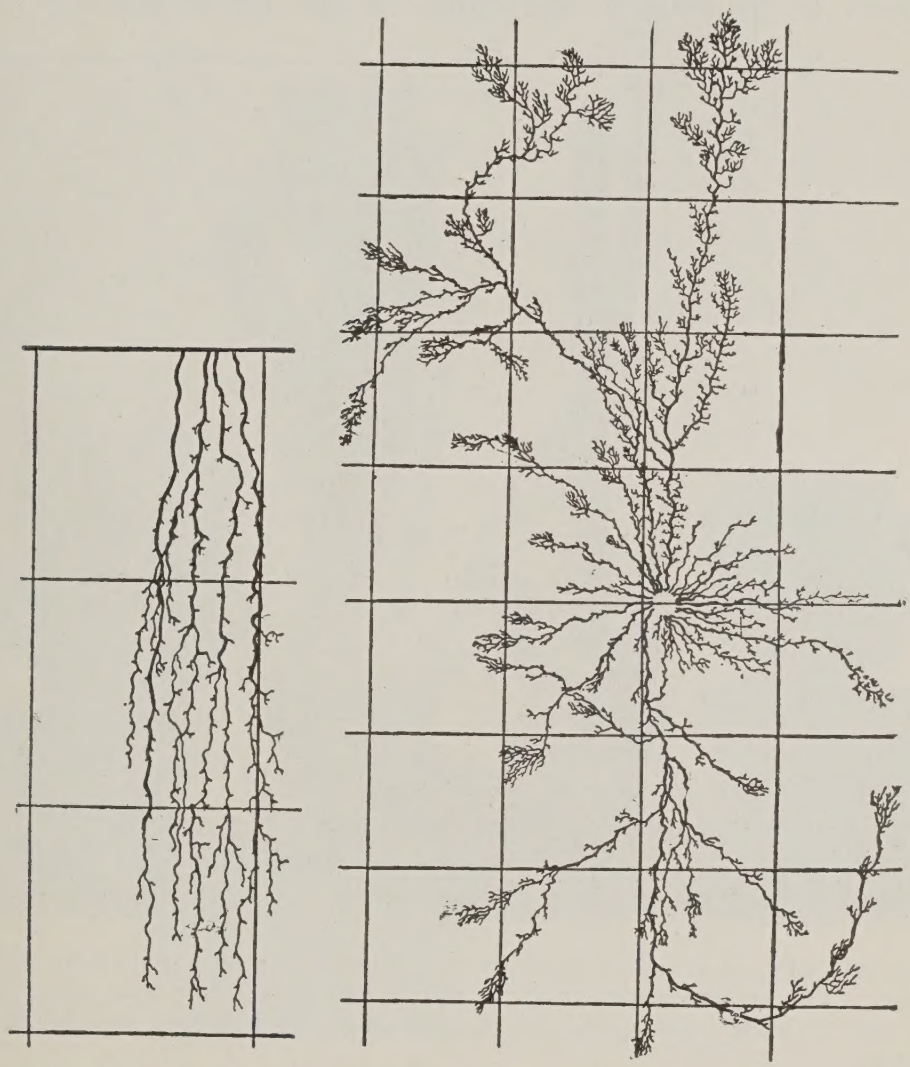


FIG. 63.—Root-system of a cactus (*Opuntia camanchica*). At the left the vertical anchorage roots. At the right is shown a top view of the surface roots, showing the wide lateral spread of as much as 6 ft. (After Weaver.)

The stems of certain species of *Euphorbia* are also modified as water storage organs and often closely resemble cacti in general appearance (Fig. 64). Their retention of water is doubtless favored by the presence of a milky juice (*latex*, not present in cacti), and by the thick cuticle over the surface, as in cacti.

Transpiration in both cacti and Euphorbias, as in numerous other forms, is also reduced by the fact that they often possess no leaves.

The edible stemmed grape (*Vitis quadrangularis*), of tropical Africa, Arabia, and the Moluccas has succulent, four-angled stems with a thick cuticle and wing-like projections at the angles (Fig. 65). It much resembles a spineless cactus, and the stems are said to be cooked and eaten in its native regions. The

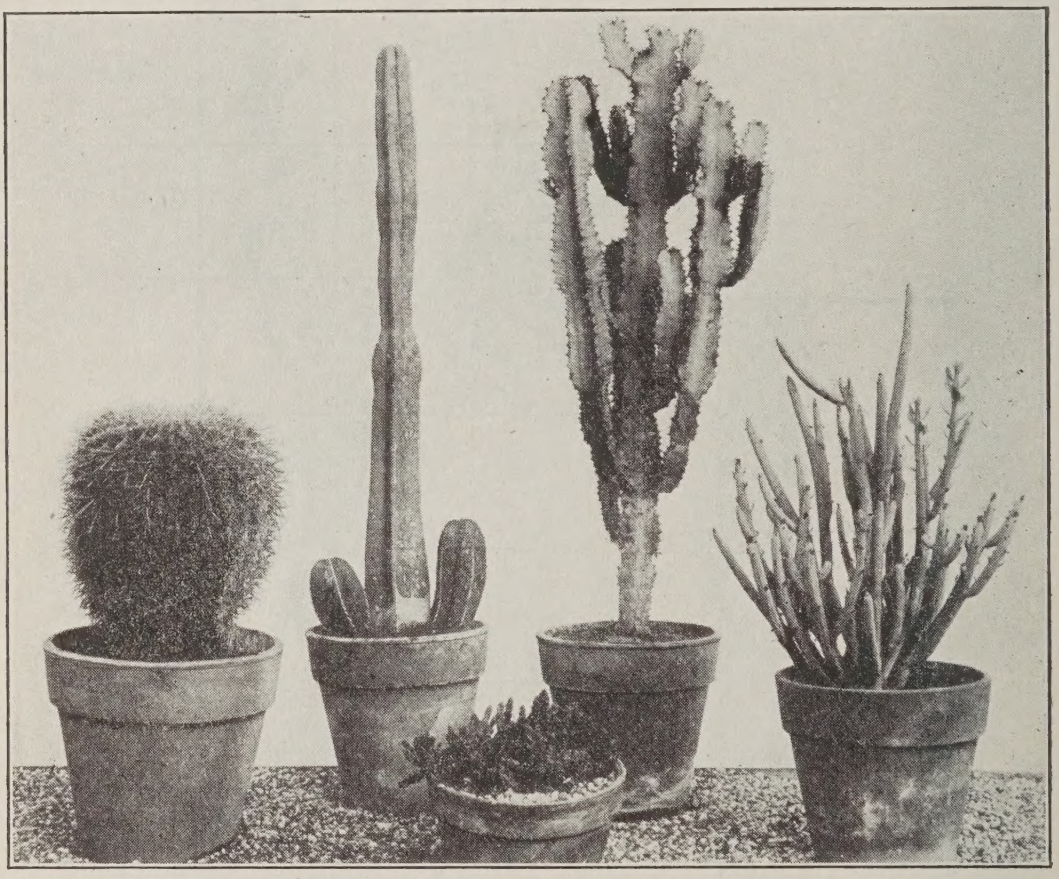


FIG. 64.—Types of desert vegetation with stems serving as organs of water storage. The smaller plant in front is *Stapelia variegata*. The taller plants, from left to right, are species of *Echinocereus*, *Pachycereus*, *Euphorbia*, and *Kleinia*.

number and size of the leaves are also greatly reduced; often it is leafless.

In many plants the leaves are modified as water-storage organs. The common houseleek, the stone-crop, century plant, kleinias, mesembryanthemums, aloes, and gasterias may be cited as illustrations (Figs. 64–66). In such plants the mesophyll tissue has a group of cells specially modified for water storage, and the

epidermis is also modified so as to prevent or greatly retard the loss of water by transpiration. In the *Hohenbergias* and *Billbergias* the stiff horny leaves are arranged on the very short stem so as to form, near the surface of the soil, a chalice or cup, which holds water (Fig. 67). The leaves of most plants, not being

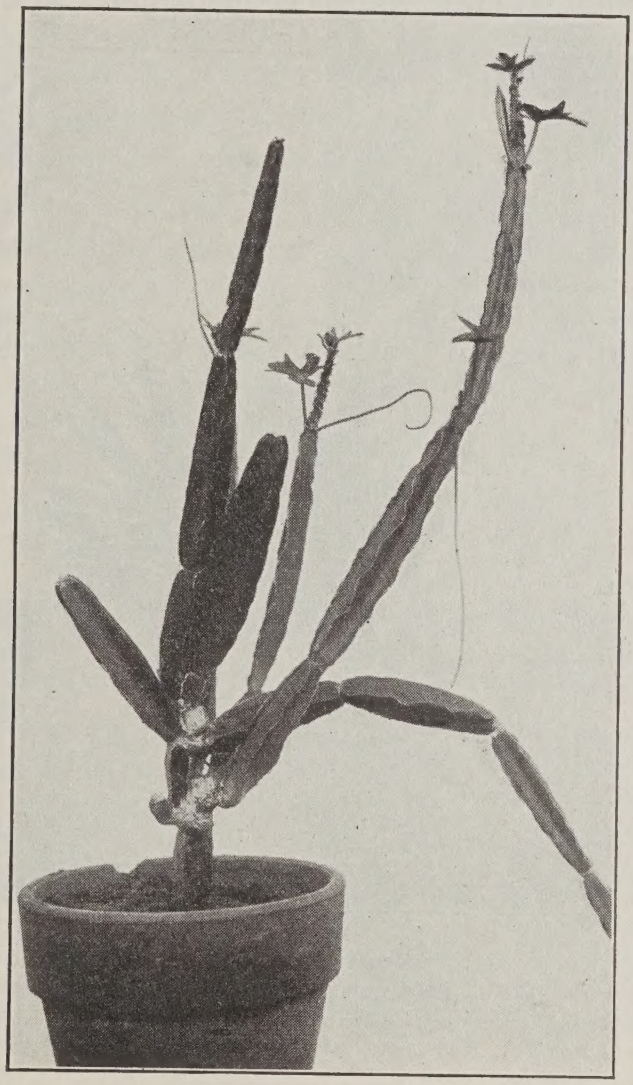


FIG. 65.—A small, potted plant of *Vitis quadrangularis*, a grape of tropical Africa, Arabia, and the Moluccas. The stem serves for the storage of water. Note the reduced foliage; also the tendrils, characteristic of the vine.

modified in this way, would decay or die if their bases were so constantly immersed in water.

Several species and genera of plants have leaves modified as "pitchers," which hold water. In the pitcher-plants, *Nepenthes* and *Sarracenia*, it does not appear that the water in the

pitchers serves as a source of supply for the plant, the pitchers playing another role in the plant's economy; but the case is quite different in certain species of the genus *Dischidia*, which bear leaves modified as pitchers. The pitchers of *Dischidia rafflesiana* Wallich, for example, have been described by Groom[1] and by Scott and Sargant.[2] This genus belongs to the milkweed

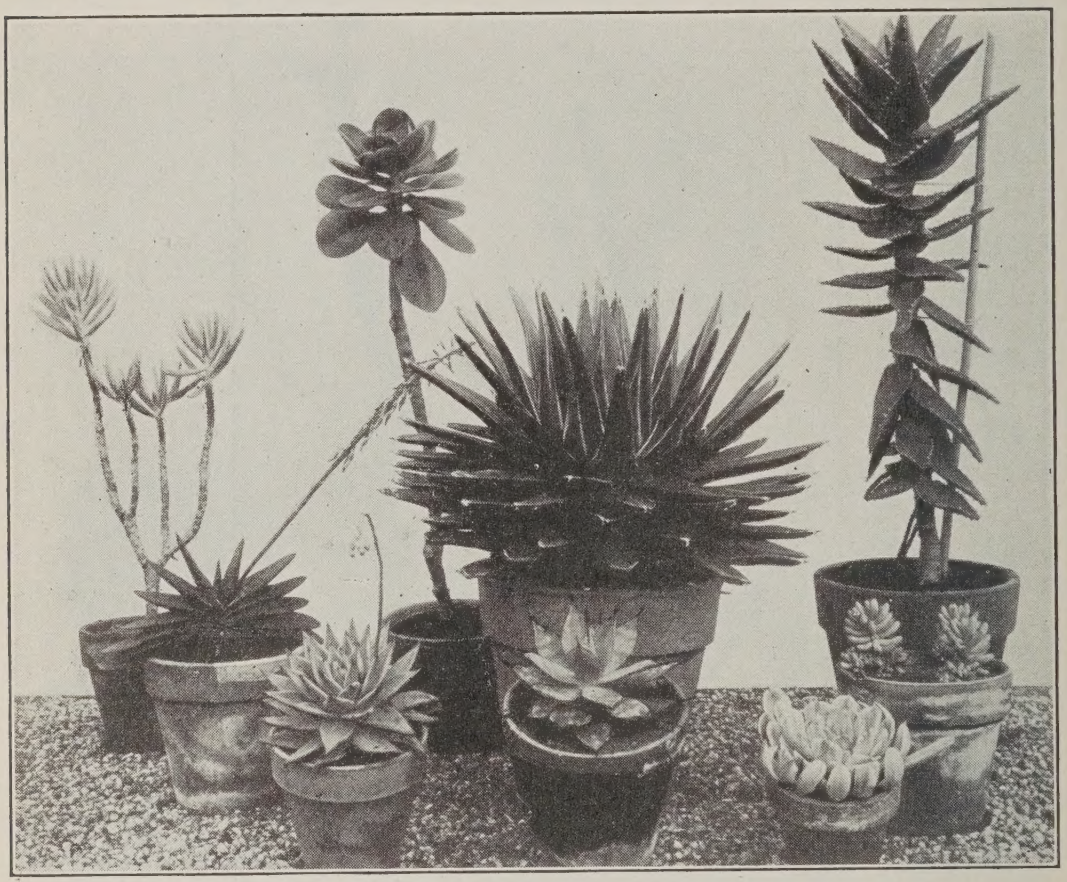


FIG. 66.—Types of desert vegetation with leaves modified as water storage organs. From left to right: front row, *Cotyledon agavoides*, *Agave* sp., *Cotyledon Hovei;* second row, *Gasteria nigricans*, *Agave Victoria-Reginae*, *Sedum Treleasei;* third row, *Kleinia ficoides*, *Echeveria gibbiflora metallica*, *Aloe distans*.

family (Asclepiadaceae), and is confined to the old world tropics. *Dischidia rafflesiana* is a twining epiphyte,[3] growing preferably

[1] Groom, Percy. On *Dischidia rafflesiana* (Wall). *Annals of Botany* **7**: 223–242. June, 1893.

[2] Scott, D. H. and Ethel Sargant. On the pitchers of *Dischidia rafflesiana* (Wall). *Ann. Bot.* **7**: 244–269. June, 1893.

[3] *Epiphyte:* a plant that grows on another plant. The term is usually confined to plants that do not derive any nourishment from the plant on which they grow, in contrast to *parasites* (which are also epiphytes).

on decaying trees, attaching itself by means of *adventitious roots*. Its choice of dead trees insures it a larger supply of rain water than it would have on trees covered with foliage, and the loss of water is prevented by a thick cuticle overlaid with a coating of wax. Even the inner surface of the pitchers is covered with wax. A second kind of roots grow from the stem and petioles down into the cavity of the pitchers where they ramify, and absorb water as from a cistern (Fig. 68). The mature pitchers are about four inches long, and the greatly branched roots within them absorb, not only water, but also nutrient substances dissolved from the solid matter washed and blown(?) into the pitchers, and brought there by ants, often forming a "soil" at the bottom of the pitcher.[1] From the standpoint of the water-relation the interesting fact is that the inner surface of the pitchers has over twice as many stomata per square unit as the outer surface, and is the chief transpiring surface. The water in the pitchers is derived mainly by the condensation of that given off as water-vapor in transpiration. Thus the same water may be absorbed over and over again.

FIG. 67.—A potted plant of *Billbergia thyrsoides*. The pot has been tipped to one side, thus spilling out some of the water lying between the leaves.

The storage of water in roots is not so common as the storage in stems and leaves. The eucalyptus tree, a native of Australia but now widely introduced in the warmer regions of America, stores water in its roots to such an extent that the natives fre-

[1] Scott and Sargant refer to the pitchers as "natural flower-pots."

quently resort to it as the source of a cool refreshing drink. The water, which drips from short lengths cut from the roots of one of the species, has no unpleasant taste, and is clear and cool. The root-tubers of the South African grape, *Vitis capensis*, serve for the storage of water as well as food (Fig. 69).

In all cases of water storage, whether in roots, stems, or leaves, the plant is able to draw on the stored supply, as on a reservoir, and is thus able to *endure* the drought without either escaping or evading it.

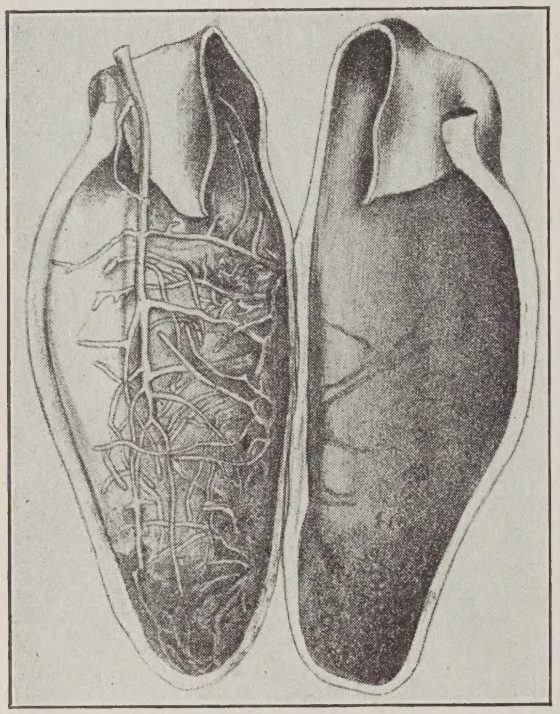


FIG. 68.—Longitudinal section of pitcher-like leaf of *Dischidia rafflesiana*, showing the roots which grow from the leaf-stalk down into the cavity of the pitcher where they absorb water and dissolved nutrients.

Dormancy.—All inhabitants of the so-called temperate zones, where there is an annual change of seasons, are familiar with most forms of dormancy of vegetation since, as noted above, the winter season is, for plants, essentially a period of drought. Plants make almost no provision for avoiding freezing. Even the winter buds, contrary to a widespread misconception, will be found frozen solid on the coldest days of winter. The chief provisions for dormancy are: leaf-fall, bud-formation, the geophilous habit, the biennial habit, and the seed habit.

Leaf-fall.—By the shedding of their leaves deciduous trees and shrubs divest themselves of nearly if not quite all of their transpiring surface. In a preceding chapter attention has been called to the fact that the total leaf-surface of moderate sized trees often amounts to several acres, and this would be a source of serious danger when the ground water was frozen, unless the structure of the leaves, or their attitude or physiological condition afforded protection. Leaf-fall is accomplished at the approach of winter by the formation of an *abscission layer* of thin-walled cells at the base of the leaf. This layer is a zone of weakness,

so that the leaf eventually falls of its own weight, or is easily broken off by the wind (Fig. 70). Moreover, these cells become *suberized* by the impregnation of their cell-walls with suberin, as is the case with all cork tissue. This prevents loss of water from the *leaf-scar*, or place where the leaf was attached. In some trees, such for example, as the poplar, willow, and oak not only leaves but entire branches are dropped by the formation of an abscission layer where the branch joins the larger limb (Fig. 71). By this *self-pruning* a dozen or more leaves are shed at once, and the branches are also automatically thinned out. With the leaves gone, the escape of water by transpiration or even by evaporation from the shoot-system is reduced almost to zero, for the bark is nearly or quite impervious to water. Our deciduous trees and shrubs are literally "corked up" during the winter. In the cork-oak the corky tissue is developed to so great an extent as to be used commercially in the manufacture of bottle-corks, cork soles, cork floors, and innumerable other articles of daily use.

FIG. 69.—*Vitis capensis*, a South African grape. The root-tubers serve for the storage of water and food. (Cf. Fig. 209.)

In artificial pruning the surface left exposed by sawing off a branch is not, of course, protected by a layer of cork-cells, and if this surface is not painted over without delay, the spores of fungi, blown about by the air, may find on the moist surface suitable conditions for germination. The fungus will thus penetrate the wood and cause the tree to decay. In poor or careless pruning stubs are sometimes left so long that the wound tissue cannot grow over the cut surface and heal it. This condition is particu-

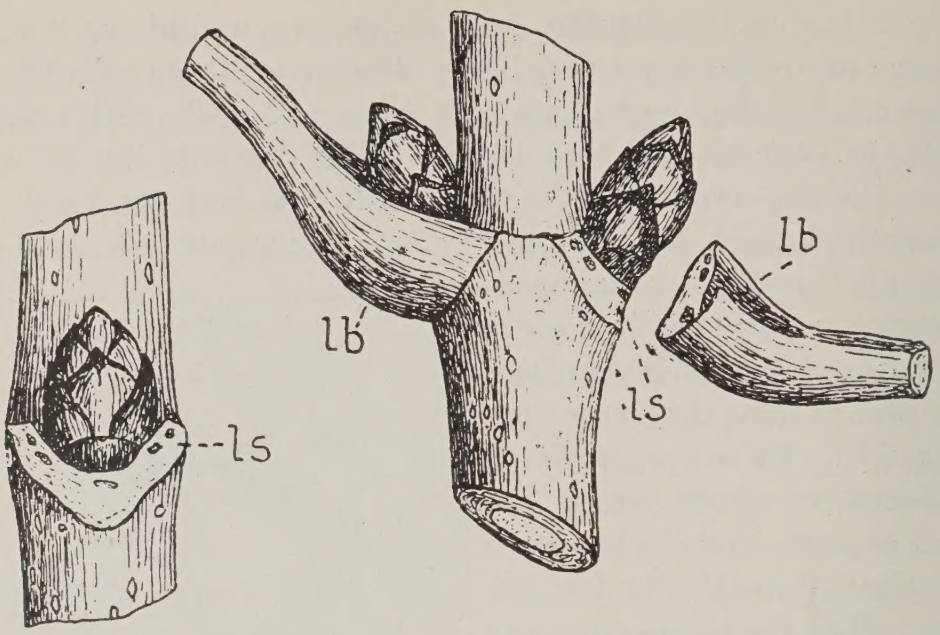


FIG. 70.—Leaf-fall in a maple. *lb*, leaf-base; *ls*, leaf-scar. (After Yapp.)

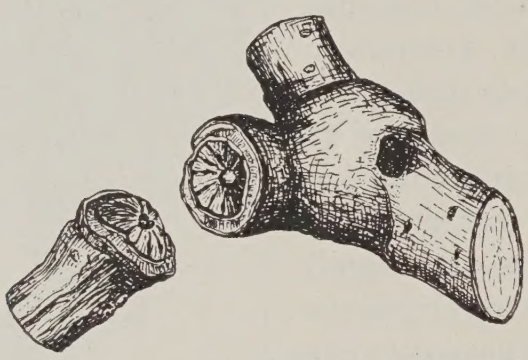


FIG. 71.—Self-pruning in an oak. The branch at the left has been self-pruned from the larger limb at the right. (After Yapp.)

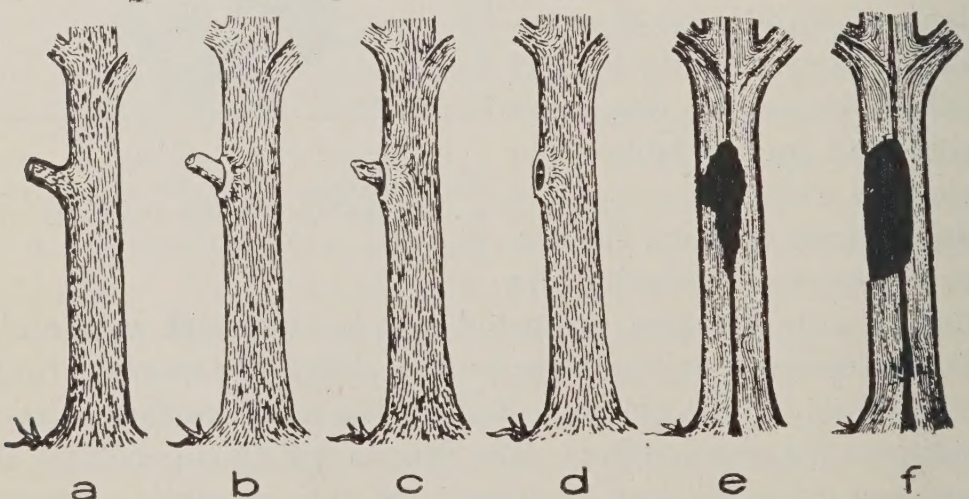


FIG. 72.—The result of bad pruning. *a*, stub left too long in sawing off the branch; *b–d*, stages in the process of decay down the stub; *e*, longitudinal section of the trunk showing cavity; *f*, cavity cleaned out (to remove the fungal threads) and then filled with cement. This treatment tends to retard the further progress of the decay. (Massachusetts Agr. Exp. Sta. Bull. 125.)

larly favorable to fungal decay which progresses from the stub down to and into the trunk, often making it hollow and ultimately resulting in the death of the tree (Fig. 72).

Bud-formation.—During the spring and early summer, deciduous trees and shrubs form true foliage leaves, but as the season advances the branch ceases to elongate and the leaves are no longer separated by the growth of *internodes.*[1] Moreover the leaves themselves are modified, developing only as dry, brown *scales,* inserted compactly, and folded over in, over-lapping so as to exclude either the entrance of water from without or its evaporation from within (Fig. 68). Often (as in the common Horsechestnut, *Aesculus Hippocastanum*) the bud-scales secrete a waxy or sticky substance which makes the bud still more impervious to water. Within, is the tender tip of the stem, with its embryonic growing point and some of the young leaves all ready to expand the following spring. Often, as in the Horsechestnut, lilac, and other trees and shrubs, there is a flower cluster, or several of them within. This entire structure is a *bud.* It may be defined as an embryonic branch, protected by *bud-scales.* Often the surface of the stem and leaves within the bud is covered with a thick growth of epidermal hairs; these hairs do not prevent the bud from freezing, but they do retard the loss of water when the bud opens the following spring. With the return of spring the sap begins to flow into the parts of the bud, and this, together with the increasing temperature, stimulates the embryonic stem to resume growth. As it elongates, the bud-scales are pushed open, the young leaves turn green and expand, and transpiration begins again. The period of drought is over.

Geophilous Habit.—Many plants pass the winter underground. This is what is meant by the "geophilous" habit. The Solomon's Seal (*Polygonatum biflorum*) may be cited as an example (Fig. 73). The thick fleshy stem of this plant grows wholly underground, and is known as a *rootstock* or *rhizome.*[2] Early in the

[1] The place of *insertion* or attachment of a leaf is a *node;* the spaces between leaves, lengthwise of the stem, are *internodes.*

[2] The underground stem, or rhizome, is a rootstock only in the sense of being a stalk to which roots are attached. It is in no sense a part of the root system, and the name, like so many common names of plants and plant parts, is a misnomer, and likely to be misleading.

spring its terminal bud, formed the preceding autumn, resumes its growth and sends up above the surface of the ground a slender, summer stem, bearing the leaves and flowers. While the flowers are producing seeds another bud is forming underground at the end of the rhizome, and by late fall this bud contains the rudiments of another leafy flowering stem, ready to expand the following spring when it is carried up to the air and light by growth. With the approach of another winter all the parts above ground again wither and die.

The Wake Robin (*Trillium*), Dog's-tooth Violet (*Erythronium*), Star-of Bethlehem (*Ornithogallum*) *Hepatica*, Bloodroot (*Sanguinaria*), Lily-of-the-Valley (*Convallaria majalis*), and innumer-

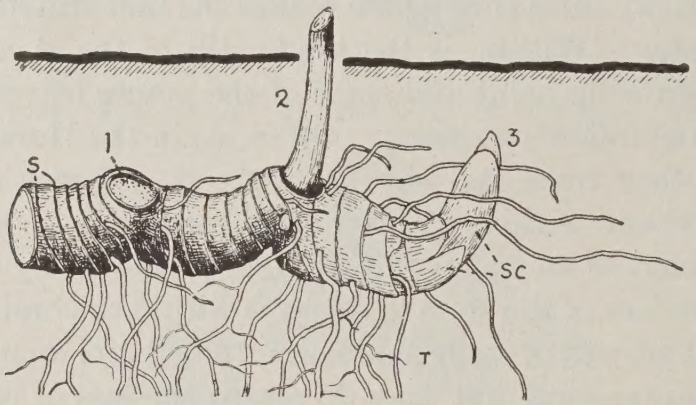


FIG. 73.—Rootstock of Solomon's Seal (*Polygonatum biflorum*). 1, scar of last year's aerial shoot; 2, base of this year's shoot; 3, Terminal bud of next year's shoot. *sc*, scale leaves; *s*, scars of old scales; *r*, adventitious roots. $\frac{5}{8}$ natural size. (After Yapp.)

able other spring wild flowers might be cited as illustrating the geophilous habit. Among cultivated plants with this habit are the asparagus, potato, sweet potato, dahlia, iris, tulip, daffodil, narcissus, rhubarb (pie-plant), onion, gladiolus, grape-hyacinth, clover, teasel, and numerous others.

Rimbach[1] has illustrated the geophilous habit by the behavior of the tulip (*Tulipa sylvestris*). The bulb rests in July and August, leafless and rootless beneath the surface of the ground. At about September it puts forth twenty to thirty threadlike roots about 18 cm. long. These roots are able to absorb water from the soil, irrigated by the autumn rains, and the water is stored in the bulb. At the beginning of March of the following year the leaves appear

[1] Rimbach, A. Beiträge zur Physiologie der Wurzeln. *Ber. deutsch. Bot. Gesell.* **17**: 18. 1899.

above the ground. In specimens which bear runners these appear at the same time, and grow until May, when the bulbs which grow at their tips become free. The flowers unfold in May; in June the leaves wilt, and the seed capsule dehisces. At the same time the roots die and a new period of rest begins.

Contractile Roots.—The method by which bulbs, pips, tubers, and other underground parts are buried beneath the surface is by

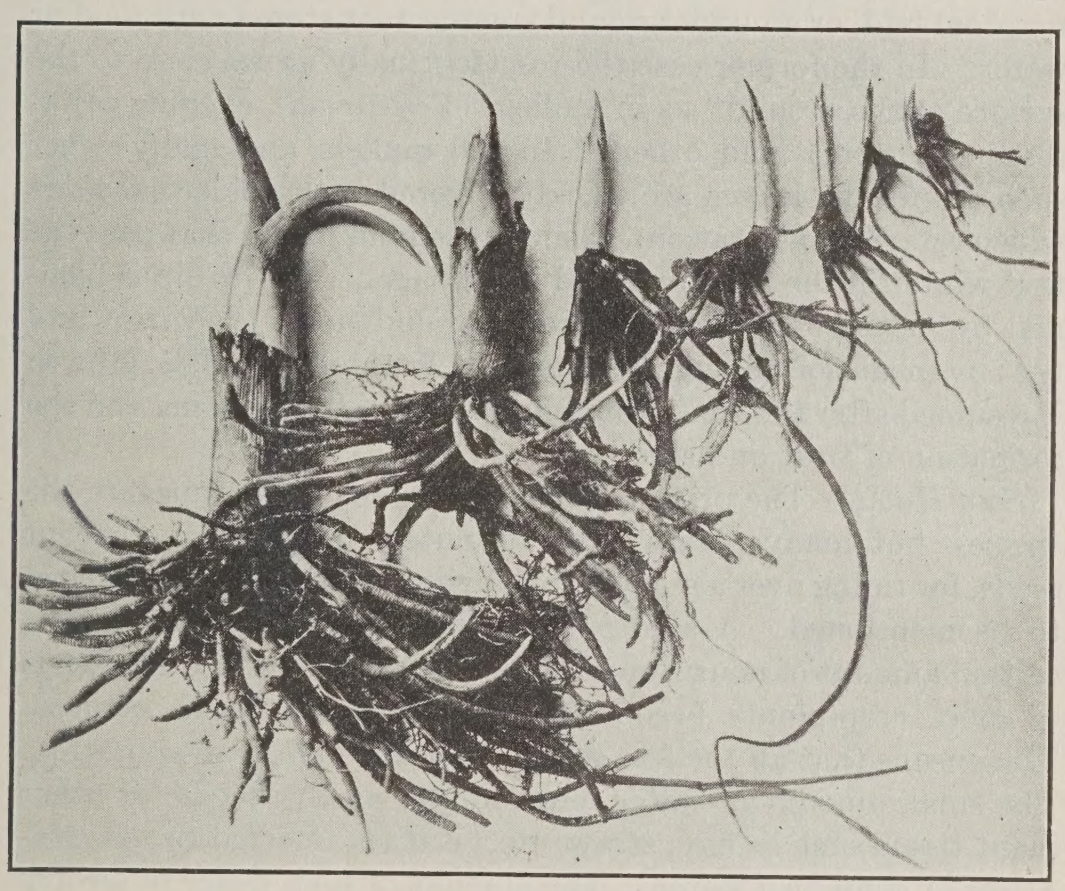


FIG. 74.—Sprouting rootstocks of Skunk Cabbage (*Symplocarpus foetidus*) carried down to successive depths in the soil (from right to left) by the action of its contractile roots.

the contraction of the roots. As the roots of geophilous species increase in length the outer tissues of epidermis and cortex elongate more rapidly than those of the central cylinder of vascular tissue. At the close of the period of active elongation these outer tissues lose their turgor on account of the loss of water. The inner tissues, previously under a state of passive stretching, are then free to contract. In doing so they cause a wrinkling of the outer tissues. The ends of the roots are, by the root-hairs,

held more firmly in the soil than are the bulbs, and pips, and as a result the latter are mechanically pulled below the surface of the soil and frequently buried several inches (Fig. 74).

Biennial Habit.—Plants which require two seasons in which to mature seed are *biennials;* they include many weeds, and many cultivated plants. The common behavior of such plants is to produce, during the first year, either a *rosette* of leaves, or a large terminal bud, or an underground stem or root stored with food or water. In the former case the rosette usually grows close to the surface of the ground,[1] as in mullein (*Verbascum*), evening primrose (*Oenothera*), and others. In the mullein and many other such plants the leaves are thickly covered with epidermal hairs which retard transpiration. Among biennial plants that pass the first winter in the form of a bud is cabbage. The turnip is biennial by means of a thickened underground stem; the carrot and beet by means of underground roots. With all biennials, growth is resumed after the winter drought, followed by flowering and the formation of fruit and seed.

Seed Habit.—The primary purpose of seeds is to propagate the species, but many plants have absolutely no provision, except seeds, for tiding over a season of drought. Examples hardly need to be mentioned. A seed is an embryo plant supplied with a certain amount of nourishment stored in or around it. The seeds of most crop-plants become *air-dry* before they are planted. This means that all the free water has passed off by evaporation. The small amount of water remaining in air-dry seeds (or other plant tissue such as hay, straw, etc.) is often referred to as *hygroscopic* or combined water. The amount of such water in air-dry seeds varies within rather narrow limits. For corn and most grains the percentage is from 14 to 14.5%. The garden bean and red and white clover have about 15%, while in oily seeds the percentage may fall to as low as 11.8% in flax and 7.7% in cotton.

The embryo may remain dormant, but still capable of resuming its growth (germination) for various lengths of time, depending upon the species, and the temperature and other conditions of storage. A high temperature shortens the vitality of seeds. It

[1] The first year's rosette of biennial plants is drawn down and held close to the ground by means of contractile roots.

is said that seeds of willow will not grow if allowed to become dry, and they lose their capacity to germinate within about two weeks after they become ripe. Certain conifers have seeds that will not germinate until they have lain dormant two or more years, while the red clover (*Trifolium pratense*), common locust (*Robinia*

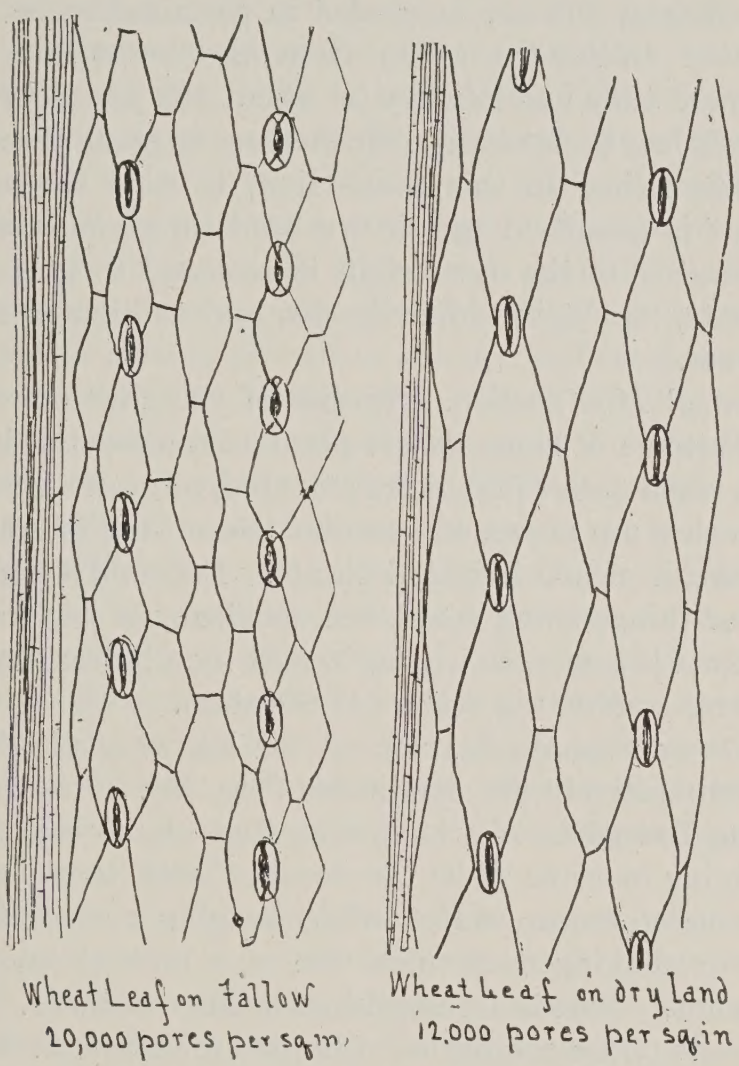


FIG. 75.—At the left a strip of leaf epidermis of wheat growing on summer fallow; there are 20,000 stomata per square inch. At the right a similar strip from wheat growing on dryer land; there are only 12,000 stomata per square inch. (After V. W. Jackson.)

Pseudoacacia), and several other plants, bear two kinds of seeds, one capable of germinating the first year, the second only after two or three years of dormancy. We know that the seeds of the mangrove tree (*Rhizophora Mangle*) commonly germinate while still in the ripened ovary attached to the parent plant, and exces-

sive late rains are often injurious to wheat, oats, barley, etc., by causing the grain to "sprout" while the plants are still standing in the field. Tales of the germination of grain found with Egyptian mummies have been conclusively disproved, though it has been stated on good authority that the famous English botanist, Robert Brown, succeeded in germinating seeds of the yellow lotus (*Nelumbo*) taken from the herbarium of Hans Sloan,[1] where they had lain dry for about 150 years (*Cf.*, p. 153). Wheat seeds lose their vitality within three to seven years.

It is interesting, in this connection, to note the amount of water that is absorbed by air-dry seeds in germination. This varies from 8% of the dry weight in mustard to 44% in maize, 59% in oats, 96.1% in kidney beans, and as high as 126.7% in white clover.

Anatomical Modification.—Studies of Cannon[2] on water-conducting systems of some desert plants disclosed the interesting fact that, when desert plants are irrigated, or even semi-irrigated, their branches are poorer in vascular tissue than branches of the same diameter of non-irrigated plants. It would seem from this that, other things being equal, the deficiency of water supply to desert plants is compensated for in part by a better development of the water-conducting system of the stem.

Also, fewer stomata develop on the leaves of plants growing under comparatively dry conditions (Fig. 75).

Evading Drought.—We have seen that plants escape drought by remaining inactive while the drought lasts; they endure it by drawing on stored-up water while keeping active; they *evade* drought by making economical use of a limited supply in the environment. This is accomplished in three ways: 1. By ability to germinate under conditions of limited moisture; 2. By making extra provision for absorption from a wide area by increased root-development; 3. By controlling the loss of water in transpiration.

[1] Hans Sloan (1660–1753). Secretary (1693) and president (1727) of the Royal Society. His bequest to the British government in 1753 of his library and natural history collections was the foundation of the British Museum (1759). He also presented to the Apothecaries' Company the botanic garden at Chelsea which they had previously rented. He traveled extensively in France, and brought back to England a large collection of plants which he sent to the noted botanist, John Ray.

[2] Botanical Gazette **39**: 397–408. 1905.

1. *Germination of Desert Forms.*—Livingston found that the seeds of some desert plants (*e.g. Fouquieria splendens*, and the giant cactus) can germinate in soils slightly drier than those required by such forms as radish (*Raphanus sativus*), red clover (*Trifolium pratense*), and the cultivated balsam (*Impatiens*), but the difference is not marked. Thus the percentage of soil water by volume required for the germination of the desert forms mentioned was found to be 15–20%, while the percentage required for *Impatiens* was 20–25, for radish 20 or more, and for red clover 25% or over. Moreover, while the development of the shoot of desert forms, after germination, is slow, the primary root grows in length with great rapidity, and thus the absorbing surfaces are rapidly carried to depths below the surface where water is always present in amount sufficient for growth.

2. *Exceptional Root Development.*—Trees, shrubs, and certain green fodder plants often extend their roots to a depth of many feet. The roots of alfalfa (lucerne, *Medicago sativa*, will penetrate to a depth of many feet in open soil.[1] In fact, during the first season after sowing the seed, the strength of alfalfa plants goes chiefly to the making of the root system, so that the first season's crop is comparatively small. The roots of certain trees extend to really remarkable depths; those of the common locust or false acacia (*Robinia Pseudo-acacia*) have been known to reach a depth of 50–60 feet. The olive tree, which will grow in exceedingly dry situations, evades drought by sending its roots down to a depth of many feet.

3. *Reduction of Transpiration.*—The most efficient water-economy is secured by conserving the water absorbed by the roots and, since the principal organs of transpiration are leaves, this may be secured by reducing the leaf surface. In such plants as cacti and some of the euphorbias the reduction is complete.

Partial reduction of leaf-surface is secured by reducing the size of the leaf-blades (as in heather, asparagus, pine, hemlock, arbor-vitae, and most conifers), by the rolling-up of the leaves during drought (oleander, rhododendron), and by the so-called "sleep" movements. In some of the acacias the leaf-blade fails of development altogether after the first few leaves of the seedling;

[1] It has been stated that in certain soils the roots of alfalfa have extended to a depth of 40–50 feet.

and the petiole, somewhat expanded and flattened, performs all the functions normally cared for by the blade, except that transpiration is thereby greatly reduced (Fig. 35). The so-called "sleep" movements are characteristic of leguminous plants, like bean, clover, alfalfa, locust, and others (Fig. 181).

The presence of essential oils, gums, and resins, as in pitch pine, camphor, and eucalyptus, and the milky juice or *latex* of such plants as milkweed, lettuce, fig, euphorbia, mulberry, poppy, papaw (*Carica papaya*), and others, serve the plant by helping to retain the moisture. Latex not only tends to hold water, but coagulates rapidly when exposed to the air, and thus quickly closes all wounds and prevents loss of water. The presence of these substances is no doubt also, in some cases, a protection against the plants being eaten by animals.

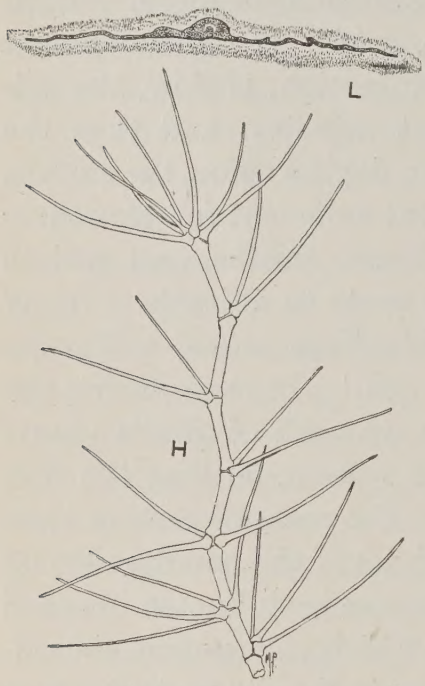


FIG. 76.—Mullein (*Verbascum Thapsus*). L, cross-section of leaf-blade, showing relative thickness of layer of epidermal hairs; *H*, a single hair from a leaf (greatly magnified).

Loss of water is further retarded by the presence of a waxy secretion on the surface—such as the "bloom" on cabbages, grapes, and many other plants. The waxy covering of the fruit of the gourd, *Benincasa cerifera*, is so abundant that it is used by the natives of India for making candles. Epidermal hairs (Fig. 76) and cork also serve a protective purpose. The cork "jacket" of the cork oak is a striking example of the latter type of protection. Evaporation from apples is retarded largely by a waxy secretion of the skin, while a similar protection of the potato tuber is secured by a layer of cork cells in the skin.

The arrangement and attitude of leaves on the branch often operates to reduce transpiration. Thus in the so-called "compass plants" (*e.g.*, the wild lettuce—*Lactuca scariola*—Fig. 77) the leaf-blades are commonly arranged approximately in a north-south plane, thus exposing the edge of the blade to the direct rays of the sun throughout the hottest part of the day. The leaves

of arbor-vitae overlap throughout the year, while in spruce and some other evergreens the leaves fold in together so as to overlap during the drought of winter.

Many plants are aided in withstanding drought by having the number of stomata reduced, or by having sunken stomata

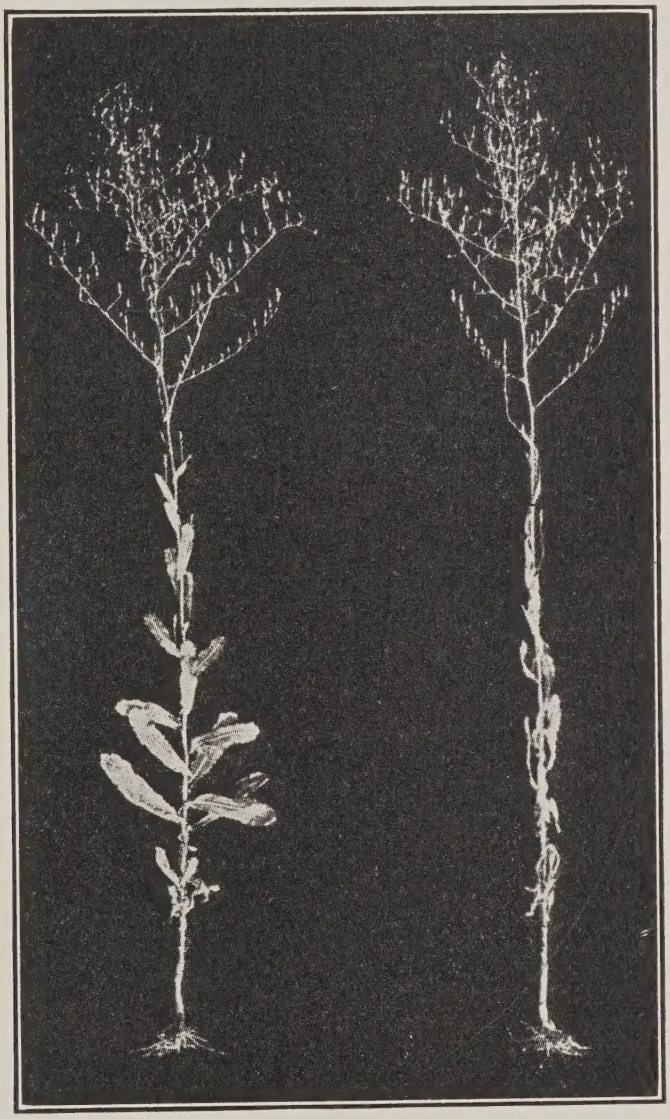


FIG. 77.—A "compass plant"—wild lettuce (*Lactuca scariola*). At the left a plant as viewed facing east or west, the leaves occupying approximately a north-south plane. At the right the same plant viewed facing north or south. (After J. C. Arthur.)

(Figs. 78–80). The habit of the entire plant often helps to reduce transpiration. This is the case with the dwarf willows and conifers of alpine summits. Often the willow trees above the timberline will be only a few inches high, although they may be many

years old. In such cases, too, the leaves are greatly reduced in size. The low stature results in less exposure to the drying

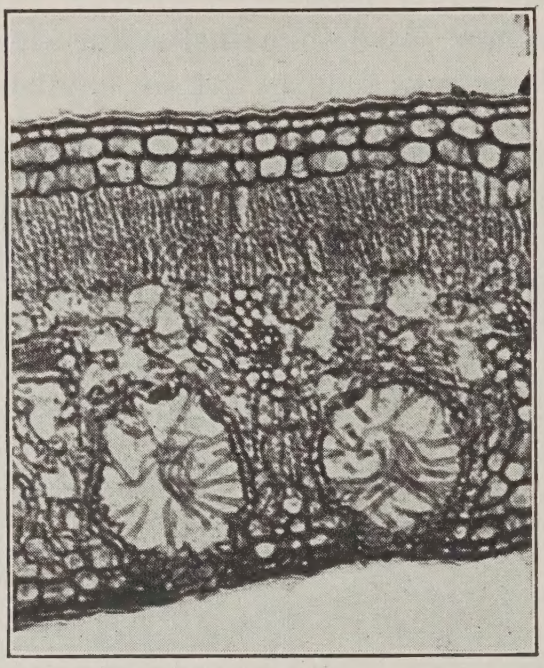


FIG. 78.—Photomicrograph of a cross-section of a leaf of oleander (*Nerium oleander*), showing two stomatal cavities lined with epidermal cells, and opening through the surface of the leaf. The stomata are in this epidermal lining, and the cavities are partly filled with epidermal hairs which help to retain water vapor within the cavities.

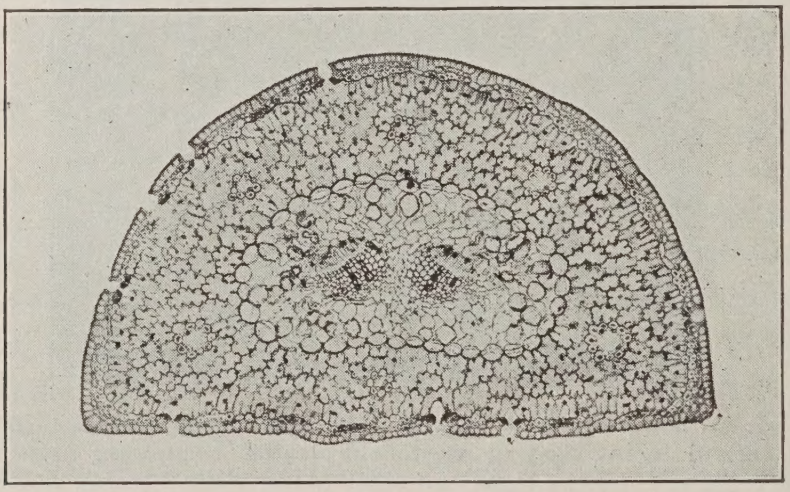


FIG. 79.—Photomicrograph of a cross-section of a leaf of a pine, showing several stomatal cavities. The more darkly stained cells at the bottom of these cavities are the guard cells of the sunken stomata.

winds, and enables the plant to benefit from the protection of shade from rocks.

A most striking illustration of the modification of a crop-plant, which fits it for successful cultivation under arid or semi-arid conditions, is that of the Hopi and Navajo maize, so called because cultivated by the Hopi and Navajo (and also the Zuñi) Indians in Arizona and New Mexico. This variety is of a low water requirement (a good drought-resisting character), and differs from the commoner varieties of maize in the germination of its seed. All other known varieties develop three roots at the same time from the embryo in germination (Fig. 81), but the

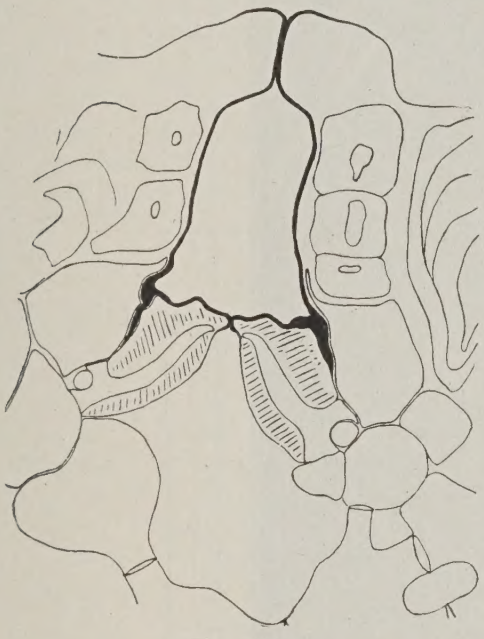


Fig. 80.

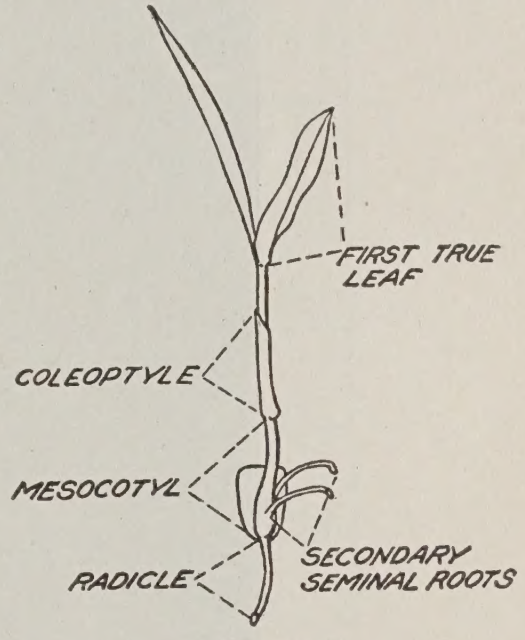


Fig. 81.

Fig. 80.—Diagram of a section through a stoma of *Cycas normanbyana*, showing the chamber under the guard-cells, and also a chamber above them, and closed by the projection of the epidermal cells until they meet. (After Rehfous.)

Fig. 81.—Seedling of Indian corn (*Zea Mays*), showing the three seedling roots and the names of the parts.

seedling of the Hopi maize possesses but one root. All the root-producing strength thus goes into this one organ which consequently develops with great vigor. In addition to this last characteristic, the *mesocotyl*, a portion of the main axis, peculiar to maize and other grasses (Fig. 81), attains a length as great as 36 centimeters, or about three times its average length in other varieties of Indian corn. By the rapid elongation of mesocotyl and seedling root, the latter soon reaches the moist subsoil, thus insuring a supply of water until the summer rains afford sufficient

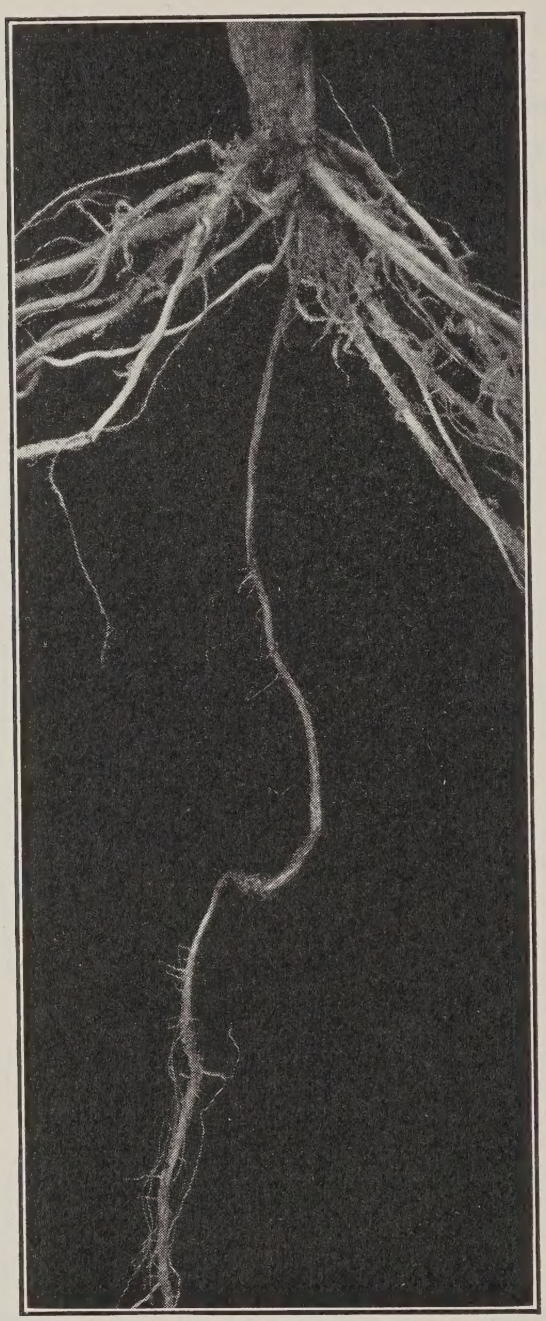


FIG. 82.—Root system of a plant of Zŭni maize dug from a field near Zŭni, New Mexico, showing the well-developed single seed-root, and the comparatively feeble nodal roots. The surface of the ground is at the level where the main root system emerges. The abrupt bend at the upper end of the deep, vertically growing seed-root is the locus of the seed-grain, and the portion from there up to the base of the stalk is the *mesocotyl* (middle portion of the cotyledon). This plant was dug from the field shown in figure 85. Slightly reduced in size. (After G. N. Collins.)

moisture in the upper layers of soil for lateral roots to develop nearer the surface (Fig. 82). Were it not for these characteristics maize could not be grown on the windy table-lands of that region, for the soil moisture resulting from the winter rains soon disappears, and if planting were delayed until the summer rain fell, the season would be too short to mature the crop.

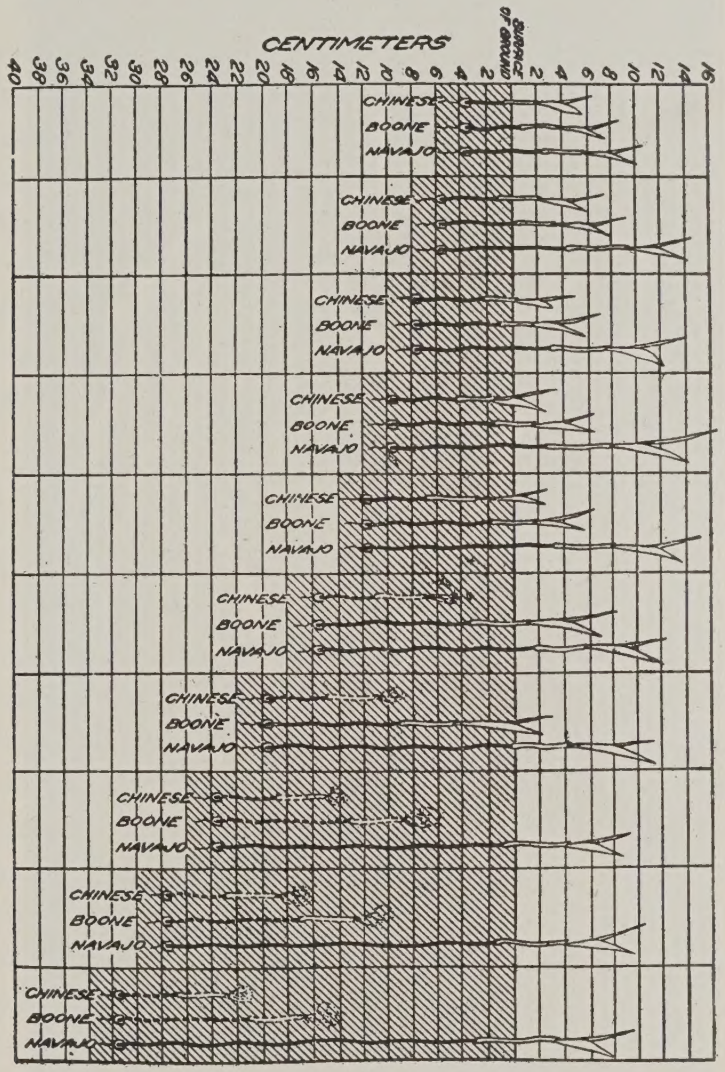


FIG. 83.—Diagram showing the average size of seedlings of Chinese, Boone County White, and Navajo maize planted at different depths. (After G. N. Collins.)

"In planting their maize," says Collins,[1] "the Hopi Indians dig into the sandy soil until they reach moist earth, usually found at

[1] Collins, G. N. Tropical varieties of maize. Washington, 1917. A drought-resisting adaptation in seedlings of Hopi maize. *Jour. Agr. Research* **1**: 293–302. Jan. 10, 1914.

a depth of from 6–18 inches. The seed is deposited in the holes in contact with the moist soil. Although these holes may be

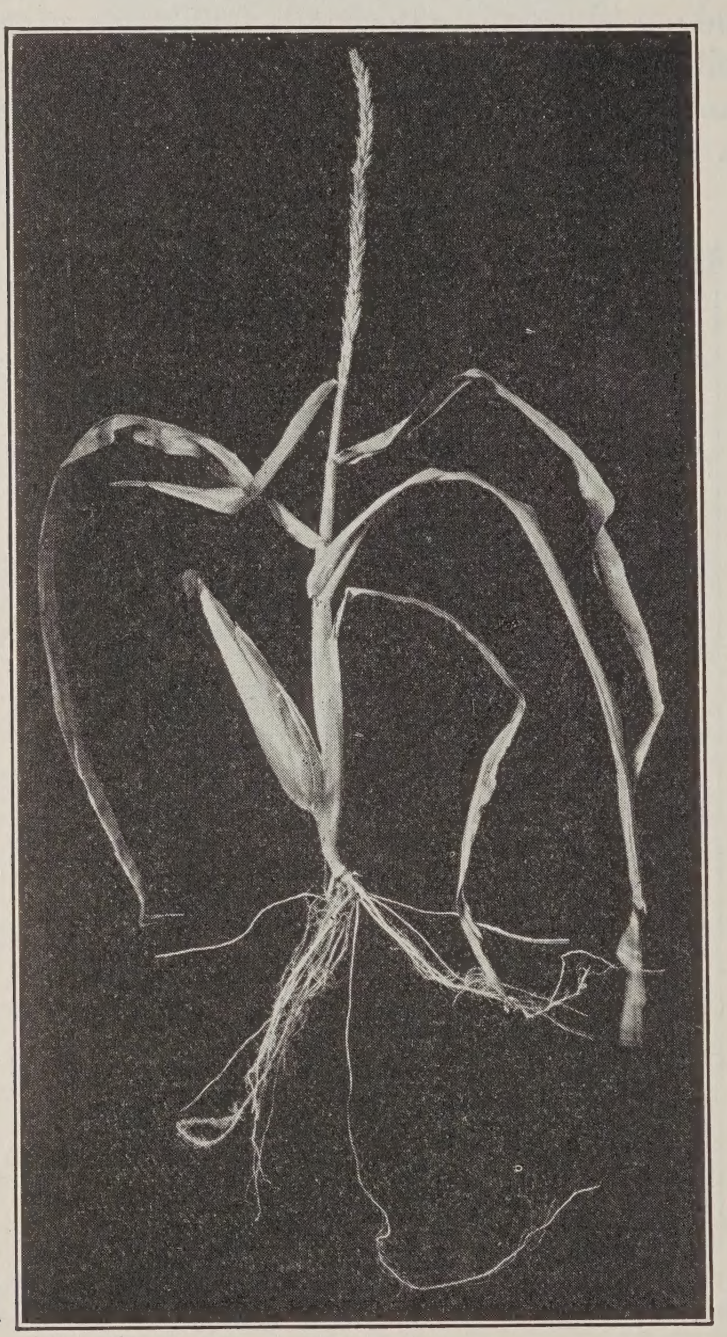


FIG. 84.—A plant of Hopi maize. Note the ear which has formed very near the surface of the ground. The remains of the seed-grain are scarcely visible at the sharp bend of the mesocotyl, 25 cm. below the surface. (After G. N. Collins.)

left only partly filled, the drifting sand soon fills them, and to reach the surface the young plants must penetrate from 6 inches to a foot of soil." The contrast in the behavior of Hopi or

Navajo seedlings and those of other varieties when planted at various depths is illustrated in figure 83.

The mature plants average only about 5 feet in height (Fig. 84), and moisture is further insured to each plant by spacing the hills as far as 20 feet apart, with 10–20 plants in a hill (Fig. 85). Under irrigation, Navajo maize is commonly planted 2 feet apart in the row, with the rows 4 feet apart.

It hardly needs to be stated that combinations of the above features are often found in the same plant; the sorghums, for example, are cited by Kearney and Shantz as both drought enduring and drought evading.

Agricultural Practices to Overcome Drought.—1. *Irrigation.* The most effective method of reclaiming arid regions for agriculture is *irrigation.* In general this term designates any method of supplying water to plants, and is often used in connection with overhead systems which supply a kind of imitation rain from a system of perforated pipes installed at a distance of five or six feet above the ground. Such irrigation is of value only in regions where the average rainfall is sufficient, but where temporary drought of several weeks at a critical period may threaten the success of the crops.

In regions of permanent drought the only effective irrigation is that whereby a copious supply of water is supplied by streams conducted in artificial water courses or ditches, whence it percolates or soaks downward and laterally (Fig. 56). This method is now so thoroughly and widely understood as to need only brief mention here. As Hilgard[1] has pointed out, the countries which have harbored most of the ancient civilizations are regions of deficient rainfall and compulsory irrigation, and the practice can succeed only where there is a high degree of civilization with its attendant cooperation, coordination, engineering skill, legal regulation, and respect for and obedience of the laws.

As an example, there may be mentioned the plain of Cheng-tu, China, which "is said to have one of the finest and most ancient systems of irrigation in the world. It was perfected about 200 B.C. by Li Ping, who has since become the patron saint of Cheng-tu . . . He divided the Min into three great delta systems

[1] Hilgard, E. W. Steppes, deserts, and alkali lands. *Pop. Sci. Month.* **48**: 609–616. March, 1896.

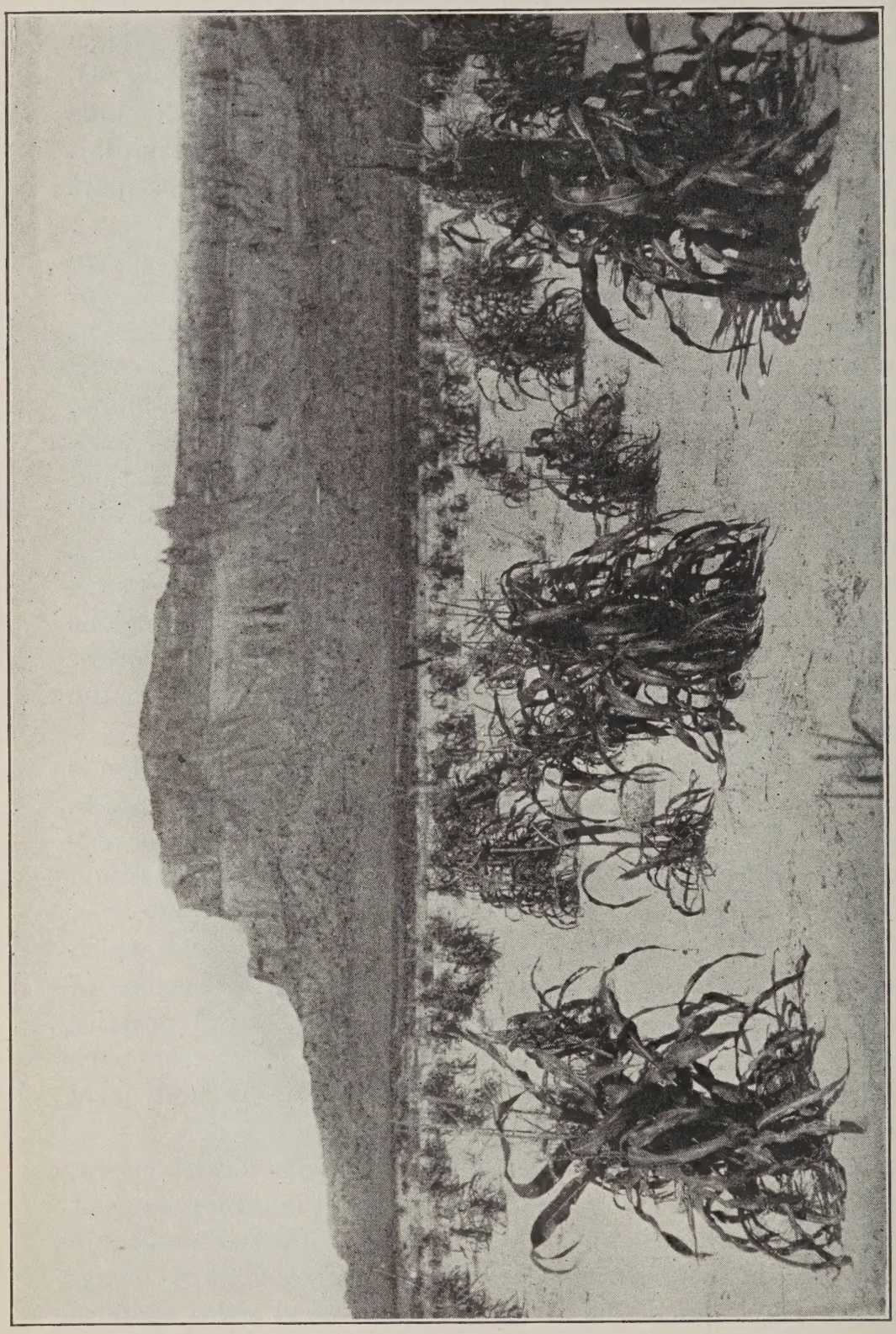


Fig. 85.—Field of Zũni maize near Zũni, New Mexico. Note the wide distances between the individual plants. The second hill from the left shows but one plant with a relatively large ear borne at the surface of the ground. (After G. N. Collins.)

of rivers and canals, which radiate to all parts of the 80 mile plain. The waters are united again in two main streams, which leave the southwest and southeast borders of the plain by the Min and the Lin rivers. He left the people this motto for regulating the canals: 'Keep the banks low and the bottom clean;' and this wise counsel has prevented the disastrous floods of ancient times, while furnishing a never-failing supply of mountain water for the fields."[1]

An interesting illustration of agriculture overcoming almost insuperable obstacles to crop production is the method of grape culture in the Diyalah district, northeast of Baghdad in Mesopotamia. Here grapes can be successfully grown only on land that is too high for surface irrigation, but where irrigation is the

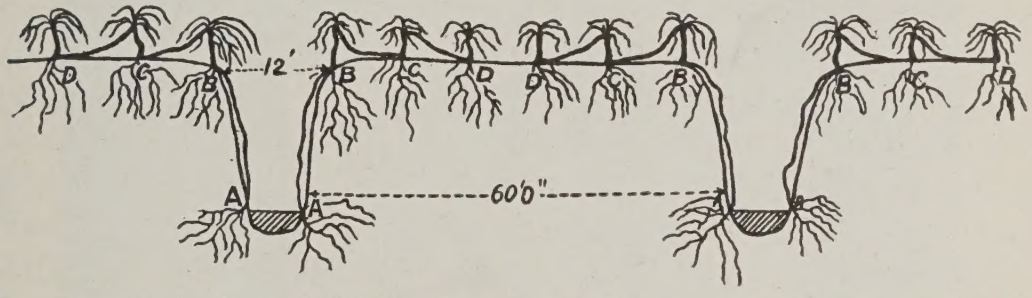


FIG. 86.—Method of irrigation of grapes in Mesopotamia. Description in the text. (After C. Gautby.)

only adequate source of water for crops. To overcome this difficulty parallel trenches are dug 60 feet apart and about 15 feet deep. This depth is sufficient to enable the irrigation water to enter from the main canal. A grapevine is planted at A (Fig. 86), at the level of the water. It is then layered at the top of the trench (B), and kept pruned to bush form. From this bush, when formed, a single branch is allowed to grow to a length of 12–15 feet, and then layered at C. This process is repeated until three bushes are developed, all supplied with water absorbed chiefly by the root-system of the original plant near the bottom of the irrigation ditch.

2. *Conservation of Forests.*—One of the most important practices for the conservation of water is the conservation of forests, and the reforestation of denuded areas. This is a matter of the greatest economic importance.

[1] Beech, Dr. Joseph. The eden of the flowery republic. Nat. Geog. Mag. **38**: 355–374. Nov. 1920.

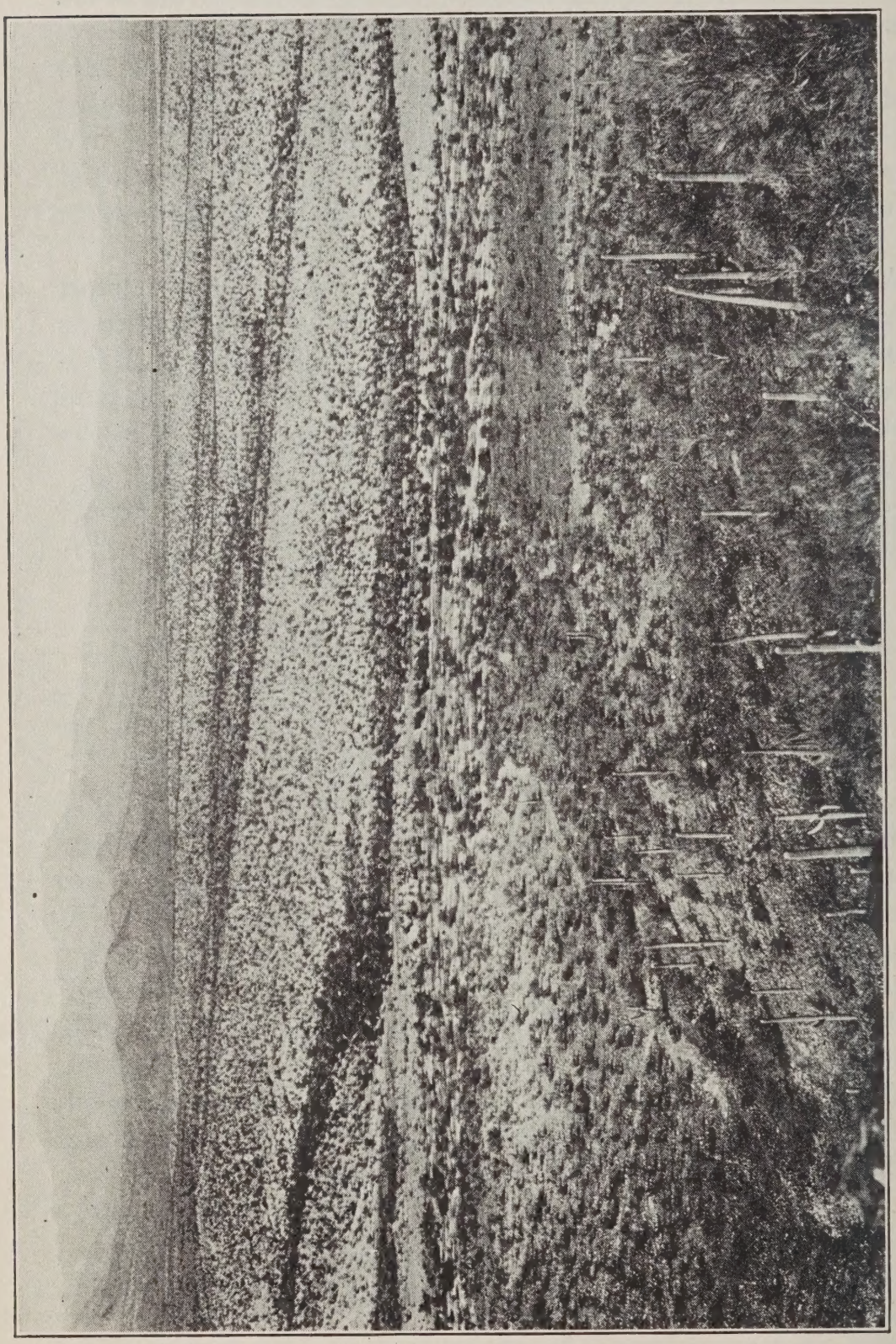


FIG. 87.—View near Tucson, Arizona, showing a strictly desert type of vegetation consisting of giant cactus (in the foreground), palo verde, ocotillo, creosote bush, prickly-pear cacti, chollas, etc. Note the comparatively wide spaces between the plants. (After Coville and MacDougal.)

3. *Thin Stand.*[1]—In deserts and other very arid regions the vegetation is sparce, the larger plants especially standing wide apart, thus reducing the competition of their roots for the limited moisture in the soil (Fig. 87). By imitating this with cultivated plants the same advantage is secured (Fig. 85). It is said that the failure of crops in arid regions has often been due to a too thick stand. Thus, in southern Tunis, near the northern edge of the Sahara, a profitable olive crop is secured by planting only seven to eleven trees to the acre. For California, Pierce (*Year Book*, U. S. Department of Agriculture, 1896) recommends that, from the start, trees be set 30 feet apart.

4. *Intertillage and Pruning.*—Severe cutting back of the branches of orchard trees and cultivated nut trees, or removal of some of the leaves (as in *Citrus*, p. 646), will reduce the leaf surface, and thus the loss of water by transpiration, while tillage between the trees will not only give a "dust mulch," which retards evaporation from the surface of the soil, but will also prevent competition with the trees by destroying the grass and weeds, and thus eliminating the loss due to transpiration from thin foliage.

5. *Thorough Tillage.*—As the frontier of civilization moved westward from the humid regions bordering the Mississippi River to the more arid regions of the(plains, the same methods were followed that had brought fair success under more favorable conditions of soil and abundant rain. Plowing was infrequent, and shallow fields were left in stubble, and commonly the grain was even "stubbled in" upon the unplowed stubble of the preceding year's crop. It is a well-known fact in agriculture that an unplowed field, with the stubble of the last crop still standing, affords the most favorable condition for loss of soil moisture by evaporation, and, of course, this loss is all the greater under conditions of prevailing high temperature and winds, such as characterize the semi-arid middle western United States. It is therefore essential to turn under the stubble as soon as possible after a crop is harvested, and to plow deep enough to afford a reservoir sufficient to retain a maximum amount of the water that falls as

[1] In the remainder of this chapter the author has drawn freely from Kearney and Schantz, *Year Book of (U. S.) Department of Agriculture for* 1911.

rain. There are various other precautions and practices of tillage to be followed, but this is not the place to go extensively into such details. (*Cf.* p. 129.)

6. *Choosing Drought-resistant Crops.*—As in the case of wild vegetation, certain cultivated plants are more drought-resistant than others, and naturally one should choose such crops for an arid or semi-arid region. Kafir corn, milo, durum wheat, and "sixty-day" oats are mentioned by Chilcott as illustrations of such crops.

Natural Vegetation as an Indicator for Crops.—The Bureau of Plant Industry of the U. S. Department of Agriculture has called attention to the fact (known to the Romans and other early peoples) that the natural vegetation of a region is an indicator of the crop-producing capabilities of new land.[1] Since the natural vegetation is the product of decades, or even of centuries, of struggle with climate and survival, it may be relied on as an indicator for the indefinite future, for the climate of a region is one of its most stable features.[2] Thus, for example, two of the so-called short grasses, grama grass (*Bouteloua oligostachys*) and buffalo grass (*Buchloë dactyloides*) are found to thrive in eastern Colorado, occupying wide areas to the almost total exclusion of all other vegetation. In this region for over 13 years the average monthly rainfall has varied from 0–0.32 inches in January to a trace–2.77 in. for July. The yearly average is 17.40 inches, with a maximum of 28.48 inches at one station in 1898. The water content of the soil is very low, and is only slightly if at all altered below the first 18 inches by rainfall. Most of the rainfall does not penetrate the soil, but is quickly removed by run-off and evaporation. Most of the loss from the soil is by the transpiration of the plants. Reference to Fig. 88 will show that the short grasses that thrive under such conditions are shallow rooted, their roots penetrating to a depth of only about 18 inches. They are also plants of short seasons. Grama grass matures in about 60 days. More-

[1] Shantz, H. L. Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area. *U. S. D. A. Bur. Plant Industry.* Bull. 201. 1911.

[2] Weather is fickle and uncertain; nothing is more uniform and unchanging than climate. Cf. p. 89.

over, these grasses may dry out, like the "resurrection plant" (a species of *Selaginella*), or like lichens, thus entering upon a rest period during extreme drought, and resuming their activity with the first light shower. The indication is clear for agriculture; a crop of deep-rooted plants, requiring a long season is foredoomed to failure, while crop plants with botanical characteristics like the short grass, given a thin stand, are likely to succeed.

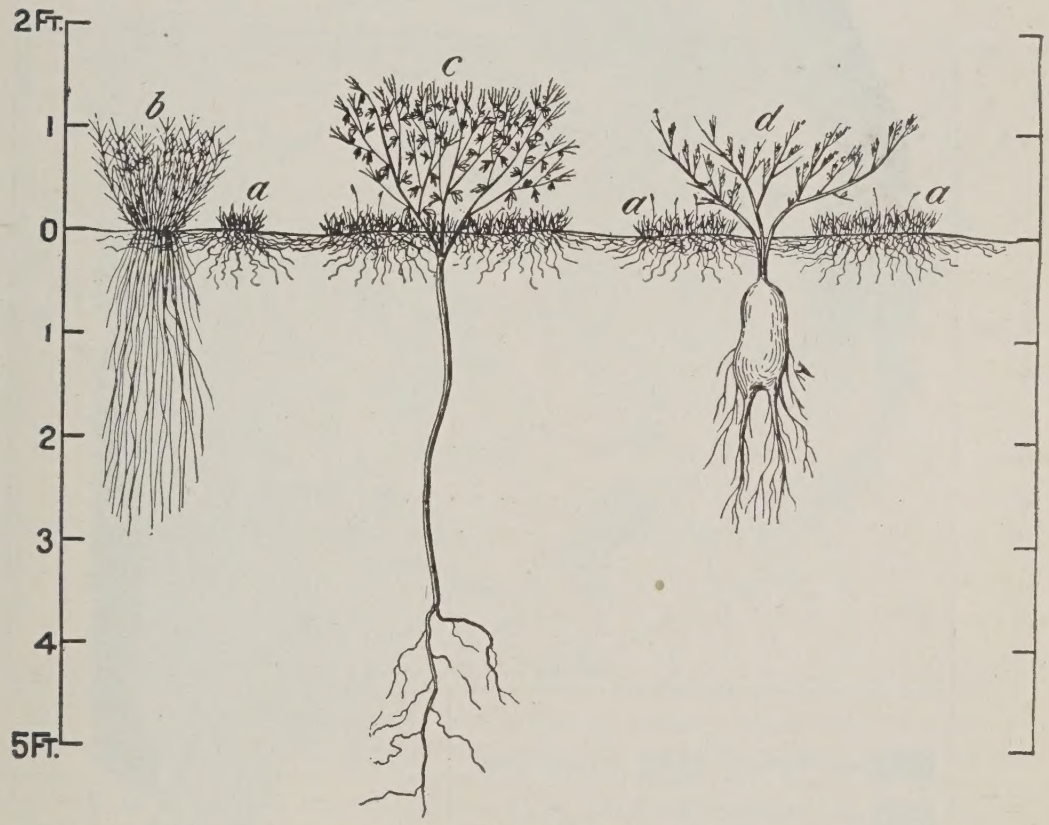


FIG. 88.—Sketch showing root distribution in the wire-grass association of an arid region. *a*, shallow-rooted grama grass, alternating with the deep-rooted mire-grass, *b*; Psoralea, *c*; bush morning-glory.

Wire grass (*Psoralea tenuiflora*) on the other hand, with roots extending to a depth of 5–6 feet, and with almost no surface-feeding roots (Fig. 88), indicates the presence of soil-water at greater depths, and therefore the probable success of a crop of deep rooted cultivated plants. But, in contrast to the soil of short-grassland, the soil of wire-grassland absorbs most of the rain that falls and is moist to a depth of several feet, so that it will also support shallow rooted crops, even better than will short-grassland.

Growing Dwarf Varieties.—Many agricultural plants, such for example, as oats, barley, sorghum, and maize, have dwarf varieties capable of giving a profitable yield, yet demanding less water from the soil and giving less to the air because of the reduction of their transpiring surfaces.

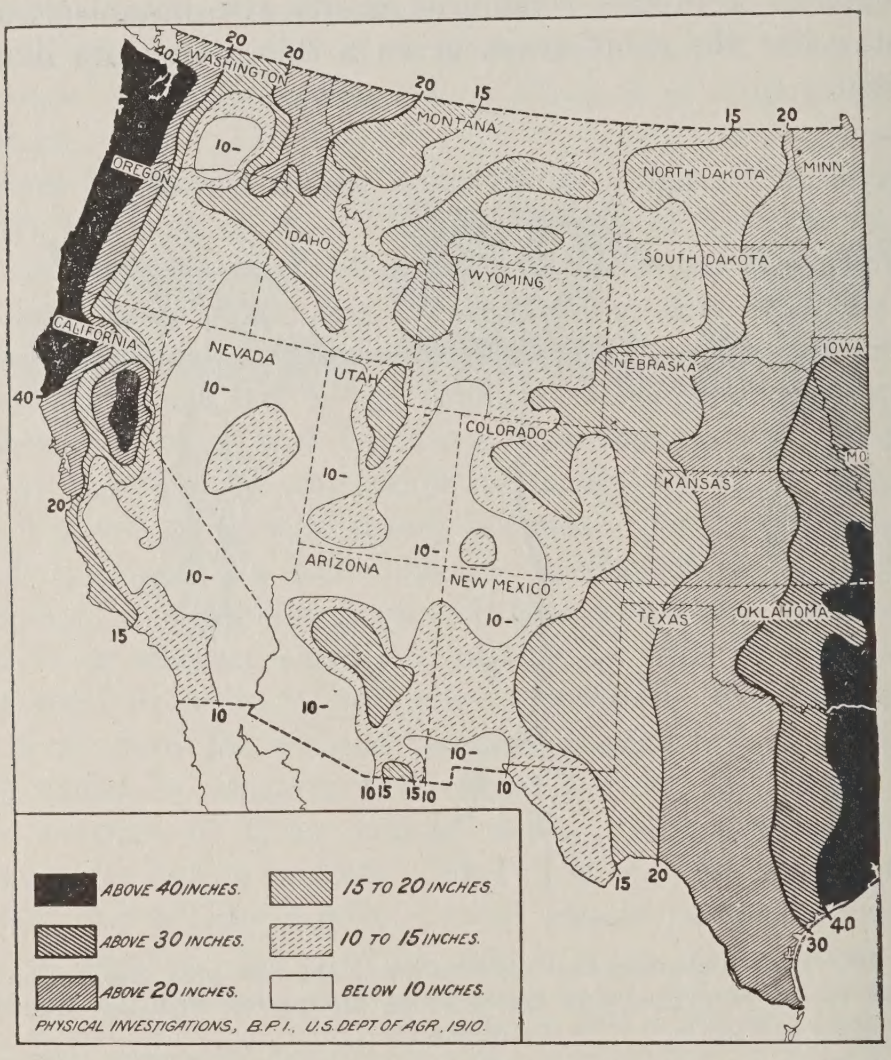


FIG. 89.—Chart showing the distribution of annual rainfall in the dry-farming sections of the United States. (After Briggs and Belz.)

Dry Farming.—On the semi-arid lands of the Great Plains area of the United States a profitable agriculture has been made possible by the practice of "*dry farming.*"[1] This area is bounded on the east by about the 98th meridian, west longitude, on the west by the 5000 foot contour line of the east slope of the Rocky

[1] Chilcott, E. C. Dry-land farming in the Great Plains area. *Year Book U. S. Dept. Agric.* **1907**: 451–468. 1908.

Mountains, and extends from the Canadian boundary to the southern part of the "panhandle" of Texas (about 32° south latitude). In general, the practice of dry farming is confined to those regions having an annual precipitation of not less than 10 and not more than 20 inches; but the distribution of the rainfall throughout the year, and the rate of evaporation are also very important factors (Fig. 89). The term "dry farming" is also somewhat relative, for the methods vary more or less with the

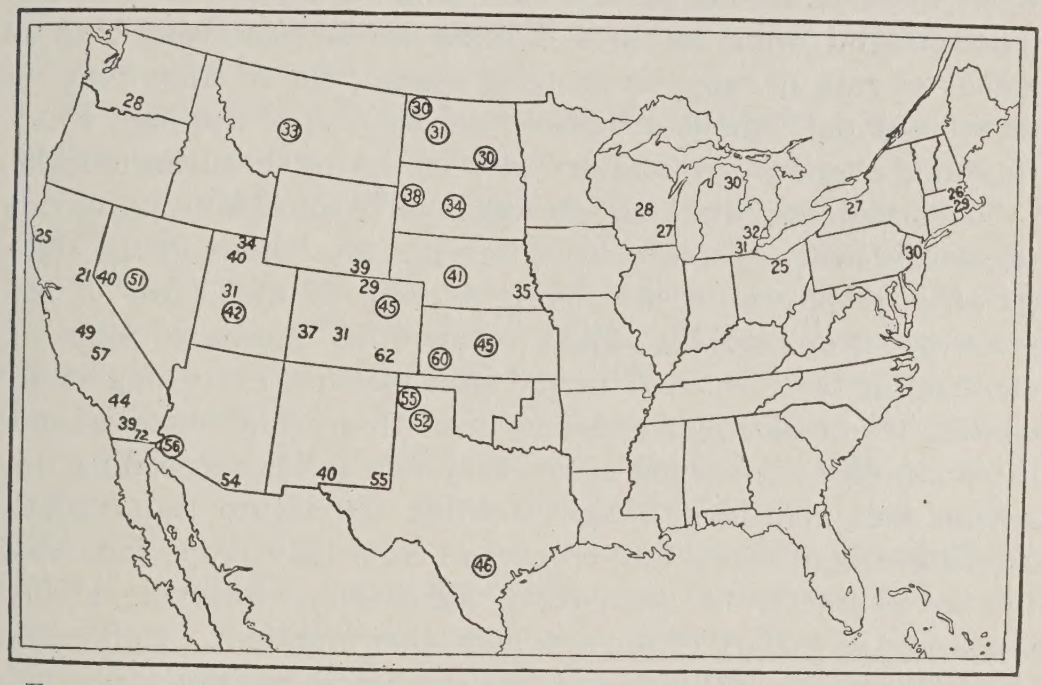


FIG. 90.—Chart showing the evaporation in inches during the six summer months from April to September, inclusive, for various points in the United States. The circles show stations where evaporation measurements are being made by the Bureau of Plant Industry, U. S. Dept. of Agriculture. The figures indicate the evaporation in inches. (After Briggs and Belz.)

actual aridity of the locality. As Briggs and Belz[1] have pointed out, crops are often a failure in the Eastern United States owing to conditions of drought where the dry farmer, with modern methods, would have secured a good crop.

A comparison of the annual rainfall map (Fig. 89) and the chart showing evaporation (Fig. 90) discloses the fact that over the region just mentioned much more water is lost by evaporation in

[1] Briggs, Lyman J. and J. O. Belz. Dry farming in relation to rainfall and evaporation. *U. S. D. A. Bur. Plant Ind. Bull.* 188. Washington, 1911.

the six summer months (April to September) than falls as rain during the entire year. The greater the loss by evaporation, the less effective for agriculture are any given number of inches of rainfall. By summer-fallowing methods it has been demonstrated that wheat can be grown at a profit in southern Washington where the annual rainfall varies from 8.5–10 inches. At Edgeley, in southeastern North Dakota, in 1908, with only 9 inches of rain during the growing season, 13 bushels of wheat were raised on spring plowed land, and 16 bushels on summer-fallowed land; while at Hays, Kansas, in the same year, with 14 inches of rain during the growing season, the average yield of wheat was only about 4 bushels, on account of the high winds (favoring evaporation) and dry weather during the spring months.

The practices of dry land farming involve suitable crop rotation (especially with reference to conserving the humus in the soil), plowing quickly after harvesting a crop (to avoid loss of soil moisture from stubble which evaporates moisture rapidly), compacting the surface of the soil after plowing, harrowing before seeding (to break up any surface crust from which water evaporates rapidly), harrowing after every rain following seeding (for reason just mentioned), light seeding (to secure thin stand), growing drought-resistant crops and especially crops indicated by the character of the native vegetation, preserving a *dust mulch* on the surface of the soil, and other practices. In fact the chief objects of cultivation of the soil are to maintain a mulch and to keep down weeds and grass whose competing roots rob the cultivated plants of water, and whose transpiration helps to dry out the soil.

Deep Tillage.—Whitney[1] enumerates the following as the four principal reasons for plowing: 1. To enable the soil to absorb rain more quickly; 2. To retain more of the rainfall near the roots of the plants; 3. To admit fresh air to the roots; 4. To enable the roots of young and rapidly growing plants to penetrate the soil more readily.

The practice of subsoiling, deep tilling, and even of soil dynamiting, especially in the Great Plains region of the United States, has been recommended and practiced to some extent as a means

[1] Whitney, Milton. Reasons for cultivating the soil. *Year Book U. S. Dept. Agric.* **1895**: 123–130. 1896.

of combating drought or increasing the yield in arid regions. Investigations of Chilcott and Cole[1] have shown the fallacy of this practice. As they point out, the root systems of cultivated plants are well distributed in the soil and subsoil of these regions to a depth of three feet or more. If necessary in order to reach sufficient soil-moisture, the roots will penetrate to a depth of five or six feet. The roots of winter wheat have been found to extend as deep as six or eight feet. Prairie soils are also fertile at such depths. The need and supposed value of deep tillage as a means of overcoming drought is therefore held by this author to have little foundation in fact.

How Soil Water Is Made Accessible to Roots.—Water exists in the upper portion of the soil in three conditions, as follows:[2]

1. *Hygroscopic Water.*—Absorbed by the soil particles from the water vapor of the air. The drier and finer the soil particles the more water will be thus absorbed. The water condenses in thin films on the surfaces of the soil particles, and is not available to plants. The absorbing power of the roots cannot overcome the force with which the water-films adhere to the soil particles.

2. *Capillary Water.*—This is the free water which is held in porous soil. Capillary attraction prevents the water settling under the pull of gravity. This water may move by capillarity from more moist to less moist regions, but it moves so slowly that the process is considered practically useless in bringing water up from lower depths for the use of crop roots. Burr found that plants will suffer or die under extreme conditions of drought after having used the available water within reach of the roots, even though there is plenty of capillary water in the soil immediately below. Even in several months capillary water will not pass upward in sufficient quantity to be of value to thirsty crops. Water, then, is made accessible to roots chiefly by their growth into moist soil. Their *hydrotropism* (see p. 285) is of the highest importance here.

3. *Gravitational Water.*—As soil becomes nearly saturated its weight (due to the pull of gravity) overcomes its surface ten-

[1] Chilcott and Cole. Subsoiling, deep tilling, and soil dynamiting in the Great Plains. *Jour. Agr. Research* **14**: 481–521. 1918.

[2] Following Burr, W. W. The storage and use of soil moisture. Bull. Agr. Exp. Sta. Nebraska. Research Bull. No. 5. July 1, 1914.

sion and adhesion to the soil particles. It then settles or percolates downward toward the free water, and tends to raise the level of the water-table. If the ground water is at a great depth the gravitational water probably never reaches it, but percolates downward until the capillary attraction overcomes the pull of gravity.

CHAPTER VII

FERMENTATION

Importance of Fermentation.—All fermentation is induced by substances known as *enzymes*, which have the power of causing marked chemical changes in other substances without being thereby permanently transformed or used up themselves. The number of different kinds of enzymes now known is very great, and it is probable that further investigation will reveal still others not now recognized. One of the most interesting and illuminating results of their study is the revelation of the fact that *one or more kinds of ferments or enzymes are produced by every living cell* (plant or animal), and that life itself involves, and is in large measure dependent upon, a series of fermentations. This truth, which is becoming more and more firmly established by scientific research, was recognized as early as 1839 by Schwann one of the founders of the cell-theory.[1] His famous work, "Microscopical Researches," contains the following passage:

"I have been unable to avoid mentioning fermentation, because it is the most fully and exactly known operation of cells, and represents, in the simplest fashion, the process which is repeated by every cell of the living body." In fact, a knowledge of enzymes and fermentation is necessary in order to understand some of the most fundamental processes of plant physiology. Fermentation is most commonly associated in our minds with yeast.

Yeast.—Practically everyone is acquainted with yeast, which was the earliest recognized agent of fermentation. We are now most familiar with it in the form of small cakes, purchased at the grocer's for use in making bread- and other "raised" dough. Our grandparents bought it in liquid from the local baker; and in breweries and large bakeries it is used in the liquid

[1] Cf. p. 15.

form in making beer and bread. If a small piece of a "compressed yeast" cake, about the size of a pea seed, is placed with a little sugar and water in a fermentation-tube (Fig. 91), and set in a warm place, the mixture will soon begin to "work," and tiny bubbles of gas will be seen rising in increasing numbers to the top of the tube. The process which gives rise to these bubbles is *alcoholic fermentation.*

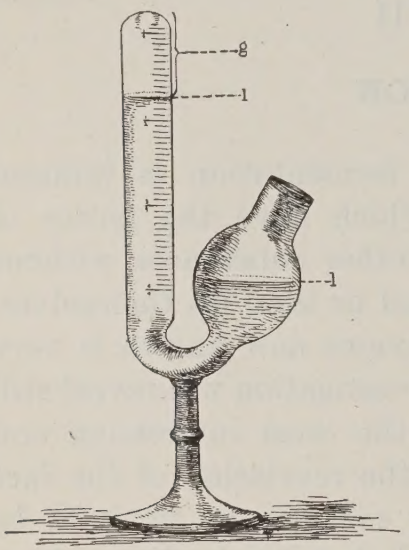


FIG. 91.—Fermentation-tube: *l*, level of fermenting liquid; *g*, space filled with gas (CO_2) given off by fermentation.

Conditions Necessary for Alcoholic Fermentation.—If two other tubes are prepared precisely like the first one, except that ice-water is used in one and boiling water in the other, and are set, the first in a cold place (*e.g.*, the refrigerator), and the second in a very warm place, fermentation will occur either very tardily or not at all. If a third fermentation-tube is set up with sugar but no yeast, and a fourth tube with yeast but no sugar, no fermentation will take place. In other words, in order to have fermentation three conditions must be realized: (1) a ferment, (2) something for the ferment to act upon, (3) suitable external conditions.[1]

Products of Alcoholic Fermentation.—If we place a large quantity of the fermenting mixture in a deep glass cylinder, and cover over the top so as to hinder the escape of the gas given off, the gas will collect in quantity in the space above the liquid. If, after fermentation has been allowed to proceed vigorously for a few hours, we insert in the cylinder a lighted splinter of wood or a lighted candle, the flame will at once go out, showing that the oxygen of the air, which supports combustion, has largely disappeared and has been replaced by another gas. The test with the flame should, of course, be made also at the very beginning of the experiment, to show that the air above the liquid will support combustion before fermentation has begun.

[1] The student may devise an experiment of his own to ascertain whether or not light is necessary to fermentation.

Carbon Dioxide Formed.—In order to ascertain what gas has taken the place of oxygen, we may next insert a fine wire, bent into a small circular loop at the end, and dipped in lime-water. A film of lime-water will extend across the space enclosed by the loop. Lime-water has the characteristic property of turning milky in the presence of carbon dioxide, and in this test the film of lime-water will at once turn white or milky, showing that the gas given off by fermentation is carbon dioxide. It is the formation of bubbles of this gas in bread dough that causes the dough to become "light" and to "rise."

Alcohol Formed.—If a large quantity of fermenting liquid—as much as a pint or a quart—is boiled, and the vapor that first comes off is condensed to a liquid, this liquid will have the characteristic odor of alcohol, and will burn with a pale, almost colorless flame. It is, in fact, alcohol, and it is on this account that this kind of fermentation is called *alcoholic fermentation*, to distinguish it from other kinds. Carbon dioxide and alcohol are, therefore, two products of the fermentation of sugar by yeast. If the proportions of yeast, sugar, and water, and the temperature are properly adjusted, and if the fermentation is allowed to continue long enough, it will be found that nearly all the sugar has disappeared, having been converted by the yeast into carbon dioxide and alcohol. Not all of the sugar will be converted for, as Pasteur, the great student of fermentation, demonstrated, small amounts of other substances such as, for example, succinic acid and glycerine, are formed by fermentation, and these finally begin to check the activity of the ferment.

Heat Produced.—If a delicate and accurate thermometer is inserted into a fermenting yeast-mixture, and the temperature recorded from time to time, it will be found that the mixture grows gradually warmer, indicating that fermentation produces heat. The experiment will succeed best if the yeast mixture is placed in a Dewar flask, or, what amounts to the same thing, in a "thermos" bottle, which is double-walled, and thus retains more of the heat produced than does an ordinary, single-walled container. It is important to keep in mind the three major results of alcoholic fermentation: (1) the formation of alcohol; (2) the formation of carbon dioxide; (3) the increase of temperature. We shall see, in the next chapter, that the last two are also the results of another important life-process of plants.

What is Yeast?—Since prehistoric times men had employed yeast in baking and brewing without having the remotest idea as to what it really was, or of how it caused fermentation. Its necessity for leavening dough was, however, clearly understood, and in the great migrations of history care had to be exercised to take along yeast in some form. In the exodus of the Israelites from Egypt (about 1451 B.C.) they departed in such haste that this important point was overlooked, and they soon found themselves under the necessity of eating unleavened bread.[1] It was not until 3000 years after that event that men began to inquire seriously into the nature of a plant so long and so intimately connected with their daily existence. In the early centuries of this period the scientific spirit of inquiry into the natural causes of things had not become general; and, even after the inquiry began, knowledge advanced slowly over a period of more than 200 years. This was due in part to the fact that preconceived notions were a hindrance to an open-minded inquiry (as has been so often the case in the history of science), in part to the slow development of the scientific method of inquiry by means of careful observation and rigid experiment, and in part to a common tendency of the human mind to turn to "authority"—to the dictum of some great name in the scientific world—in this case to the noted German chemist, Liebig.

As early as 1680 the Dutch naturalist, Leeuwenhoek, (lā-vĕn-hŏŏk)[2] examining "yeast" (*i.e.*, liquid yeast-mixture) for the

[1] Exodus XII, 34, 39. This was the origin and significance of the Jewish custom of eating unleavened bread in the feast of the passover (Exodus XIII, 3; Deuteronomy XVI, 3). The "leaven" was a bit of dough saved from a previous baking; when put into newly mixed dough the leaven would leaven the whole new batch. The yeast in the leaven was a wild yeast, as in "salt rising" bread and the old fashioned wet or "potato yeast."

[2] Anton van Leeuwenhoek. *b.* Delft, So. Holland, Oct. 24, 1652; *d.* Delft, Aug. 26, 1723. Made many observations of the microscopic structure of plants, describing their cellular structure, and thus anticipating the cell-theory. First to describe bacteria (1683). In 1686 he demonstrated, through his microscope, the passage of the blood from arteries to veins through the capillaries. First to observe animalcules (protozoa) in water. He had a passion for microscopical studies, and possessed as many as 247 complete microscopes (all but 3 with single lenses), besides 172 lenses. He was a fellow of the Royal Society (London), and Peter the Great, of Russia, honored him with a visit to see and look through his microscopes.

first time with a microscope, noted that it always contained tiny floating globules; but it was 150 years after this that the French scientist, Cagniard de Latour, discovered that yeast is a living organism. Soon thereafter another French savant, Turpin, demonstrated that *yeast is really a plant*, closely related to the fungi; and in 1839 a German botanist, Meyen, assigned yeast to a new genus of plants, *Saccharomyces*. There are over forty species in the genus, which is one of the sac-fungi (Ascomycetes see pp. 463 and 472).

It remained, however, for Pasteur[1] to demonstrate by painstaking experiments that alcoholic fermentation is caused by the life processes of yeast living out of contact with free air (*i.e.*, anaerobically). "*La fermentation est la conséquence de la vie sans air*," said Pasteur.[2] The results of his experiments were communicated to the Chemical Society and to the Academy of Sciences (Paris) in April and June 1861.[3]

The conclusions of Pasteur were rejected by Liebig,[4] as late as 1870. He interpreted fermentation as due to the motion communicated to other bodies by "animal and vegetable matters in a state of putrefaction," thus apparently taking for granted the very process whose explanation was sought. Still later (1873) the German mycologist, Brefeld, also rejected Pasteur's theory. That theory, however, rested on the most careful and accurate experiments, and has since been amply confirmed by the observations and experiments of many other investigators. The vegetable nature of yeast and its causal agency in fermentation is

[1] Louis Pasteur, one of the greatest scientists of all time, was born in Dôle (Jura) France, December 27, 1822, and died at Villeneuve-l'Etang (near St. Cloud), Sept. 8, 1895. He was the founder of the science of bacteriology, and disproved by rigid experiments the doctrine of spontaneous generation. He was the first to prove, experimentally, that infectious diseases are caused by specific microbes or germs. He made important scientific investigations in chemistry and botany, as well as in bacteriology. The centenary of his birth was universally celebrated in 1922–23.

[2] Etudes sur la Bière, Paris, 1876, Chapt. VI, *Théorie physiologique de la fermentation*, pp. 261 and 266.

[3] Pasteur, L. *Expériences et vues nouvelles sur la nature des fermentations.* Compt. Rend. Acad. Sci. Paris **52**: 1260–1264. 1861. See, also, Bull. de la Soc. Chim de Paris, 1861, pp. 30–31; 61–63; 79–80.

[4] Liebig, J. von Sur la fermentation et la force musculaire. Ann. Chim. Phys. 4th Ser. **23**: 5. 1870.

no longer considered a debatable question. The "theory" of Pasteur is now recognized as a statement of demonstrated *truth*.[1] As a result of more recent researches we now have a detailed knowledge of the structure and physiology of the yeast plant.

Microscopic Appearance.—If a drop of yeast mixture that has been fermenting vigorously is examined under the microscope, the individual yeast plants may be readily observed (Fig. 92). They are seen to be unicellular plants, globular or ellipsoidal in form, of various sizes according to age, and devoid of chlorophyll. According to Nägeli,[2] a yeast cell of average size has a volume of about .000002 cubic centimeter and weighs approximately .0000005 milligram. It is because there are such enormous numbers of these cells in a yeast mixture that it can produce fermentation on such a large scale.

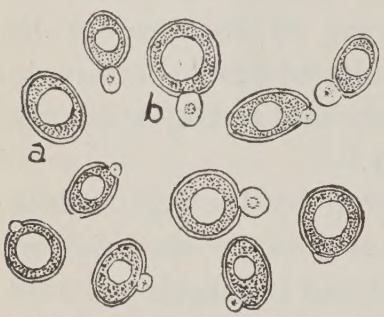


FIG. 92.—Cells of yeast (*Saccharomyces* sp.). Some of the cells are budding. The clear spaces are vacuoles.

The nucleus can be seen only after the cell is stained. Many of the larger cells will be seen to have small outgrowths or buds, also of various sizes according to age. It is by the formation of the buds, that is, by *budding*, that the plant reproduces itself. When the buds reach a certain size, they separate from the parent plant, continue to take in nourishment from the surrounding liquid by osmosis, increase in size to maturity, and then give rise to other plants, by repeating the process of budding.[3] Under favorable conditions new plants are formed very rapidly by budding, so that in the course of a few hours the total number of

[1] This is the common history of great scientific ideas. They are first put forward as a rational explanation or *hypothesis*, which points the way to further observations. When confirmed by the new evidence the hypothesis becomes a *theory*. By still further testing the theory is either disproved and rejected, or proved and then accepted as a *truth*.

[2] CARL WILHELM VON NÄGELI; Swiss botanist and philosopher. *b.* near Zürich, Switzerland, March 27, 1817; d. Munich, May 10, 1891. First to determine that all plant cells are formed from pre-existing cells. He discovered the sperms of ferns.

[3] Another process of reproduction of yeast, by the production of *endospores*, need not here be described.

yeast plants will have enormously increased, notwithstanding the fact that some of them in the meantime may have died. This increase in number may be noted with the naked eye, by observing the increase of turbidity or opalescence of the yeast-mixture after it has stood for an hour or more. The yeast cakes of commerce consist largely of starch and millions of tiny yeast plants, skimmed from the surface of a fermenting liquid, and then pressed together.

The Active Agent in Fermentation.—After it became recognized that the presence of the yeast plant is necessary in order to have alcoholic fermentation, it required careful study before it was discovered that if the yeast cells, after being disintegrated by grinding, are all filtered out of the mixture, the filtered liquid still retains the power to cause fermentation. From this it was learned that the active agent or immediate cause of the process, is not the yeast itself, but some substance or substances produced by the yeast. These substances are the real ferments or *enzymes*,[1] and are secreted by the living protoplasm of the yeast. At least three different enzymes are known to be produced by yeast. The one that is active in converting sugar into carbon dioxide and alcohol is a *zymase*, called *alcoholase;* another (*invertase*) converts (inverts) cane sugar (saccharose) into the grape sugars (glucose and fructose); a third (*maltase*) transforms another sugar, maltose, into glucose. It has been stated that invertase can transform 100,000 times its own volume of cane sugar.

Kinds of Enzymes.—Various kinds of enzymes are produced in every living cell—plant or animal. They have the remarkable power of transforming other substances without being thereby used up or permanently changed themselves; that is, they do not enter into chemical combination with the materials they transform. Following the method of Duclaux, each enzyme is commonly named from the particular substance which it transforms, and this name usually ends with the termination, —*ase*. Thus, for example, we have *maltase* which acts upon (*i.e.*, splits up the molecule of) maltose; *protease*, which acts upon protein; *lipase*, which acts upon fat, etc. This nomenclature,

[1] The term *enzyme* comes from the Greek ἔνζυμος (*enzumos*), leavened. It was first introduced by Kühne, in 1876, to distinguish these substances from the micro-organisms (such as yeast) that cause fermentation.

however, is not followed uniformly, for some of the longer known enzymes (*e.g.*, pepsin, trypsin, ptyalin, of the animal body), retain their older names, and oxidase is a term applied, not to enzymes which act upon oxygen, but to those which cause a union of oxygen with other bodies (oxidation).

Ptyalin, in the saliva, sometimes called the "animal diastase," can convert starch to sugar. This is one reason why starchy foods should be well masticated. Pepsin occurs in the gastric juice and changes the insoluble proteins of meat into soluble proteins. Lipase occurs in the pancreatic juice together with numerous other enzymes, and by hydrolysis it converts fats into fatty acids and glycerine.

Cytase.—One of the important plant enzymes is *cytase*, which can liquefy the cellulose of cell-walls. It is by this means that the delicate threads of fungi which grow on trees can penetrate the hard, solid wood. The enzyme, secreted by the fungus, softens and liquefies the wood, and the delicate fungal thread may then penetrate with ease.

When leaves fall in the autumn, the final stage in the process is the solution of a portion of the cell-walls of a layer of cells (the *abscission layer*) at the place where the leaf joins the branch. This greatly weakens the attachment, and the leaf falls, often merely from its own weight. The solution of this tissue is caused by an enzyme secreted by the cells adjacent to the abscission layer. Many of the peculiar effects produced by molds and by bacteria are caused by enzymes secreted by these organisms. The ripening of cheese, the formation of alcohol in beer and wine, the changing of sweet to sour or "hard" cider, the turning brown of cut fruit, such as apples, when exposed to the air, and all processes of decay are caused by fermentations produced by enzymes secreted by bacteria, molds, yeast, or other living cells.

The Nature and Mode of Action of Enzymes.—The fact that certain life processes are accomplished by enzymes was first recognized and taught nearly 300 years ago by Van Helmont, though, of course, he did not employ the term enzyme, nor did he have a very clear conception of these substances, nor indeed of the substances on which they act. Previous to his time it was supposed that digestion in the alimentary tract was caused by the heat of the body or by acid in the stomach, or by some

imaginary inherent property of the food to digest itself. In his chapter on the "Conception of a ferment" (*Imago fermenti*), Van Helmont refers to this teaching as folly, and elaborates the idea that digestion and other physiological processes are caused by "ferments." Our knowledge of these substances and their mode of action is still very imperfect, but the investigations of the past three or four decades have established the fact that enzyme action is not of the nature of a chemical reaction, that the enzyme does not disappear when it acts on other substances, and that the amount of the substance that can be transformed does not depend upon the amount of enzyme available. Although the action is more rapid the greater the amount of enzyme present, a comparatively small amount of enzyme is able, in time, to convert an almost unlimited amount of the substance acted on. Enzymes act, not only analytically, to break down compounds, but also synthetically, to build them up; lipase, for example, may not only split up fats into fatty acids and glycerine, but may bring about the formation of fats from those substances. Amylase is the active agent in hydrolyzing starch to sugar. Under suitable conditions it may convert sugar into starch.

According to recent interpretations, enzymes are considered as complex compounds belonging to the class of gelatinous substances known as colloids.[1] Colloids, as noted on page 50, are distinguished from crystalloids in that they will not dissolve, and therefore will not pass through a membrane by osmosis. In a true solution the molecules of the dissolved substance (either whole or separated into electrically positive or negative *ions*) move freely about, somewhat like the molecules of a gas. But the molecules of a colloid, either singly *or in groups*, are suspended in the liquid. They act, therefore, only by means of forces resident on the surfaces of these disperse particles, such as surface tension and electric charge. For example, when sugar (dextrin) is converted into starch in plant tissues, the particles of the sugar are first accumulated (*i.e., adsorbed*) on the surfaces of the particles of the enzyme (*amylase*), and then transformed into starch (*amylum*). (*Cf.* pp. 181–182.)

[1] The word colloid is from the Greek κόλλα (*kolla*), glue + εἶδος (*eidos*) semblance, meaning "like glue," glue being a typical colloid.

The enzyme acts as a *catalyzer*. Now a catalytic agent is one which, by its presence in a mixture of substances that react chemically, accelerates the reaction without entering permanently into combination—*i.e.*, without being thereby consumed. This phenomenon is called *catalysis*.[1] Substances *adsorbed* on the surfaces of colloidal particles always react more rapidly chemically, other conditions being equal.

It should be noted that some enzymes (*e.g.*, those that convert sugar into starch in the cells of potato tubers) act only within the living cell (*endo-enzymes*), while others act only after passing outside of the cells. The zymase of yeast, for example, splits up sugar into carbon dioxide and alcohol only outside of the yeast cell. The compounds resulting from this action are usually simpler (chemically) than those acted upon. In most cases the reactions are of the type known as *hydrolysis*, so called because water (H_2O) is added. The hydrolysis of cane sugar is illustrated by the following equations:

Action by Invertase

$$\underset{C_{12}H_{22}O_{11}}{\text{Cane Sugar}} + \underset{H_2O}{\text{Water}} = \underset{C_6H_{12}O_6}{\text{Fructose}} + \underset{C_6H_{12}O_6}{\text{Glucose}}$$

Action by Alcoholase

$$\underset{C_{12}H_{22}O_{11}}{\text{Cane Sugar}} + \underset{H_2O}{\text{Water}} = \underset{4C_2H_5OH}{\text{Alcohol}} + \underset{4CO_2}{\text{Carbon dioxide}}$$

Other enzymes remove oxygen from the substance fermented, *i.e.*, are *reducing agents*, while still others cause oxidation; numerous fermentations are much more complex and are not, at present, clearly understood.

Huxley's Simile.—The mystery of enzyme action has never been fully explained, but the simile used by Huxley helps us to form a crude mental picture of the process. "There can be no doubt," says Huxley, "that the constituent elements of fully 98% of the sugar which has vanished during fermentation have simply undergone rearrangement; like the soldiers of a brigade, who at the word of command divide themselves into the independent regiments to which they belong. The brigade is sugar, the regiments are carbonic acid, succinic acid, alcohol, and

[1] From the Greek words κατά (*kata*, down) + λύειν (*luein*, loose), meaning *dissolution*.

glycerine." We may add that the commanding officer is the enzyme, secreted by the yeast.

Considering the results produced, enzymes act in a truly remarkable manner. "Man," says Slosson, "takes a 1000 horse-power engine and an electric furnace at a temperature of several thousand degrees to get carbon into combination with hydrogen, yet the little green leaf in the sunshine does it quietly and without getting hot, by the action of enzymes."

The Biological Significance of Alcoholic Fermentation.—From what has just preceded, it is seen that the various processes of fermentation are useful or otherwise important to mankind, but we must seek for the real significance of alcoholic fermentation in its use to the organism that secretes the ferment. In this connection we must recall the fact that all the life-processes of plants and animals require energy. The continued release of this energy within the cells usually makes necessary a supply of free oxygen from the air; but some organisms can secure the necessary oxygen by decomposing compounds that contain it—such as carbohydrates, proteins, and fats. Thus we must regard alcoholic fermentation (in part, at least) as a process by which yeast and other organisms or cells secure the necessary energy for their activities when deprived of the free oxygen of the air. In the words of Pasteur, the fermenting character of a cell is due to the power which it possesses of respiring at the expense of sugar, out of contact with air. Alcohol and other complex compounds result because the processes of oxidation are not completed, owing to the restricted supply of oxygen that can be obtained in the absence of air. *If the oxidation processes could be completed, the end products would be carbon dioxide and water.* Organisms that may continue to live without a supply of free oxygen are called *anaerobes*.[1] Either the entire organism may live anaerobically, or this condition may be confined to one or more of its organs, or even to a single cell or group of cells. It is possible for yeast to live in contact with free oxygen, but when this is not present it can secure sufficient oxygen for its needs by alcoholic fermentation alone.[2]

[1] *an* (without) + *aer* (air) + *bios* (life) = living without air.

[2] From a reading of Chapters VII to IX the student will learn that the transformations wrought in other substances by the catalytic agents, called

Relation of Fermentation to Our Daily Lives.—Reference has already been made to the fact that such diverse operations as the manufacture of alcoholic drinks and the making of bread are dependent upon fermentations, and we shall see later on (Chapter X) that the process fundamental to all life—the formation of carbohydrates — probably involves the action of at least six different ferments. The active principles of all the digestive juices of our own bodies are also enzymes. We shall learn, in the next chapter, that all muscular and mental activity, even life itself, is dependent on the fermentative activity of enzymes.

Fermentations in Agriculture.—There is scarcely a natural process involved in agriculture and related industries that does not depend, in whole or in part, on some kind of fermentation. In the germination of seeds the insoluble stored food in or around the embryo is rendered soluble, and thereby available to the young seedling, by enzymes that dissolve starch, cellulose, fats, and protein. When potato tubers are planted, the cells of the bud or "eye" secrete a starch-dissolving enzyme by means of which the carbohydrate material stored in the tuber is dissolved. The ripening of seeds and the conversion of sugar to starch in the maturing of sweet corn are brought about in a similar way. The souring of milk, the curing of cheese, the retting of flax, the making of *sauerkraut* from cabbages, the hardening of cider and its final transformation into vinegar, the turning rancid of butter, the "ripening" of cream preparatory to churning, the transformation of ensilage in the silo, and innumerable other processes vital to successful farming and agriculture are caused by ferments secreted by living cells, often of animals, but more often of bacteria and other plants. Even the digestion of plant tissue in the first stomach of cows and other herbivora, is accomplished in large part by enzymes secreted by bacteria. Here also lies the explanation of the changes that take place in urea and stable

---

enzymes, are not all of the same nature; some (as alcoholic fermentation, and digestive processes) are destructive, others (as the polymerizations and other transformations in photosynthesis (mentioned on pages 181 and 182) are constructive. The author believes that it contributes to simplicity, without sacrificing clear and accurate thinking, to consider "enzyme" and "ferment" as synonymous terms, and to call all activities of enzymes *fermentations*, whether they are analytic or synthetic.

manure, and without which they would cease to possess their value as fertilizers. We should recall, in this enumeration, the processes of decay of roots and other plant tissue in the soil, ammonification, nitrification, and the fixation of atmospheric nitrogen, treated in detail in Chapter XII.

In 1911 Cook and others[1] reported evidence of the existence in fruits of protective enzymes, a catalase and an oxidase. Normal, uninjured fruit contains little or no tannin, but does contain a poly-atomic phenol. When the fruit (pears, apples, and tomatoes were tested) is injured by insects, fungi, or mechanical agencies, the poly-atomic phenol in the presence of an acid solution, is acted upon by the oxidase, forming a tannin or tannin-like body, and also a germicidal fluid which retards or inhibits the development of fungi and bacteria, thus hindering or preventing the decay of the fruit. The necessary conditions are always present in unripe fruits of the apple and its relatives.

It will be instructive for the student to make a list, in the order in which they occur, of the fermentations involved from the sowing of a grain of corn to the digestion of a dish of corn meal in the human stomach, or from the sowing of grass seed to the making of a pound of butter or of cheese. Other equally interesting and instructive series will readily suggest themselves.

Enzymes and the Rest-Period.—Everyone is familiar with the existence of a "rest-period" in plants. One of the most familiar illustrations of this is the winter rest of deciduous trees in the temperate zones, accompanied by leaf-fall. In cultivated plants we are familiar with it in the resting bulbs of early blooming flowers, such as hyacinth, narcissus, etc., and the winter rest of biennial vegetables such as cabbage, or the annual rest of such plants as potato, onion, sweet potato and others. Many annual plants rest only as seeds.

The cause of the rest-period is not definitely known. It is due, in part, to environmental conditions, such as the approaching cold or drought of winter,[2] and to inner changes which may directly or indirectly be due to the former. For example, the food prepared for the embryo in the corn grain is always con-

[1] Cook, Mel T., and others. Protective enzymes. Science N. S. **33**: 624–629. 1911.

[2] Cf. p. 89.

verted into starch, which is insoluble and therefore not available. The embryo is therefore obliged to rest until further internal changes favor the conversion of the starch into a soluble carbohydrate (sugar), which may be absorbed by the embryo.

As Howard[1] and others have noted, *all the phenomena connected with the rest-period are closely associated with the work of enzymes.* At first the resting condition results from the inhibiting of enzymes by the accumulation of the products resulting from their activity, *e.g.*, the transformation of sugar to starch is retarded by the accumulation of the starch. This inhibition is further promoted by the lowering temperature at the approach of cold weather, and by dessication. Often the rest-period may be broken by some condition that acts as a stimulus to the enzymes—such as ether, wounding, or subjection to higher temperature. In the latter case some plants may be made continuously active, omitting the rest-period altogether. This has been experimentally accomplished by growing oak trees from seeds in pots in the greenhouse. Under such treatment they have been made to cease shedding their leaves, and continue "evergreen." Other plants require some period of rest varying from a few weeks to a few months, according to variety or species.

During the rest-period of potato tubers some of the starch is gradually changed to sugar by diastase. This explains why old tubers often taste sweet. The result is hastened if the tubers are stored at low temperatures, and may even be experimentally accelerated by placing new tubers in a refrigerator.[2]

Most of the spring wild flowers are all formed beneath the surface of the soil by early or late fall, and require subjection to the cold of winter in order to "awaken" and resume their growth and blossoming in the spring. The low temperature appears to be necessary to stimulate the secretion of the enzymes essential to growth.

[1] Howard, W. L. An experimental study of the rest period of plants. Fifth Rept. Univ. of Missouri Coll. Agr. Agr. Exp. Sta. Research Bull. No. 21. Columbia, Mo., June, 1915.

[2] It is a general belief that freezing will cause sweetening of potato tubers, but the experimental evidence does not confirm this. The belief, as Butler suggests, is possibly due to the other belief that potatoes subjected to a temperature of 32° F. will freeze, but this has been shown by experiment, to be erroneous. In one experiment tubers were stored at 32° F. for more than 100 days, without thereby becoming frozen.

Putrefaction and Decay.—A large number of processes which are, in reality, only special types of fermentation, are designated by the terms *putrefaction* and *decay*. By putrefaction we usually mean the breaking down or disintegration of nitrogenous or protein substances, such as the bodies of dead animals and plants, cheese, eggs, *et cetera*, always accompanied by a bad odor. This process usually takes place under partial or wholly anaerobic conditions. When there is free access of air the same processes may continue, but the ill-smelling substances, such, for example, as ammonia or sulphuretted hydrogen, are either oxidized to form nitrates and sulphates, or are not formed. The process is then spoken of as decay. It is often taking place on the (aerated) surfaces of manure piles and carcases while putrefaction is going on in the (anaerobic) interior.

The bacteria that produce putrefaction are often called *saprogenic*—that is, producers of putrefaction. The process cannot take place in dry tissues, nor at certain low temperatures, hence the practice of preserving meat for long periods by drying (*e.g.*, dried beef), or by refrigeration in cold storage. But the bacterial disintegration of flesh and other substances is not a simple process; usually several organisms, various processes, and numerous by-products and end products are involved. In addition to the saprogenic bacteria which break down protein molecules by the enzymes they secrete, there is commonly present another group of *saprophile* (decay loving) organisms which live upon the products of putrefaction. The putrefaction of fruit, potatoes, and other plant tissues (poor in protein) is usually accomplished, not by bacteria, but by various fungi.

Some of the products of putrefaction are similar to vegetable alkaloids and are called ptomaines.[1] Most of them are only mildly poisonous, but many are very dangerous, especially if taken in large doses. They sometimes develop in fish and fruits imperfectly put up in tins or jars, and in decaying shellfish. All food in which ptomaines are suspected to occur should be carefully avoided. Certain bacteria, in particular the pathogenic ones that cause various diseases, secrete more powerful poisons called *toxins*.[2]

[1] Ptomaine, from the Greek πτῶμα (*ptōma*), a dead body.

[2] Toxin, from the Greek τοξικόν (toxikon), poison for smearing arrows with, from τόξον (toxon) a bow.

The question is often asked as to what becomes of all the vegetable tissue that gets incorporated with the soil. Why is the soil not clogged with it? Tons of dead leaves fall to the forest floor every autumn, enormous quantities of woody tissue in the form of roots are left in the soil after the harvesting of many crops, or the cutting down of a forest. Trunks of fallen trees are gradually buried beneath the surface. What becomes of all this material? Sooner or later it undergoes the process of decay, brought about, in this case, not only by bacteria, but also by the action of various fungi. The result is *humus*, which is the most important constituent of "top-soil," and the very foundation of all agriculture. Human industry, wealth, civilization itself are dependent, therefore, in part, upon the process of decay, brought about by enzymes secreted by tiny plants.

CHAPTER VIII

RESPIRATION[1]

Anaerobes and Aerobes.—In the preceding chapter we learned that all plants require energy for their activities, and that this energy is derived by the oxidation of substances within the cell. In the case of yeast and other organisms, when living in an atmosphere devoid of free oxygen, the necessary oxygen is obtained from compounds which contain it, by the process of fermentation, brought about by enzymes. As is well known, many organisms, such as man and most other animals, and most plants, cannot live in the absence of free oxygen; such organisms, called *aerobes*,[2] continually take in oxygen from the air. The using up of oxygen by the cells creates the need for more, and in the case of man and other mammals, the supply is obtained through the lungs by breathing. Plants, however, have no lungs, nor any organs that correspond to lungs.[3]

When oxygen is consumed by plant tissues, its pressure within the plant becomes less than its pressure outside the plant, and therefore more passes in through the stomata and epidermis by the simple physical process of diffusion.

Consumption of Oxygen Demonstrated.—The exchange of gases between the atmosphere and the interior of the plant may readily be demonstrated by a simple experiment, as follows. Into each of seven glass cylinders (Fig. 93) fit a partition of wire gauze, so as to divide the space vertically into equal parts. Into the first jar place nothing, and fill the space, on one side only of the wire gauze, in each of the other size jars respectively, with germinating seeds (pea or lupine), living herbaceous stems,

[1] Reprinted, with only slight changes, from Gager, *Fundamentals of Botany*, Chapter IX.

[2] *aero* (air) + *be* (*bios*, life) living in air.

[3] Leaves have sometimes been called "the lungs of plants." From our study of nutrition, it will be readily recognized that leaves may much more appropriately be called the stomachs of plants.

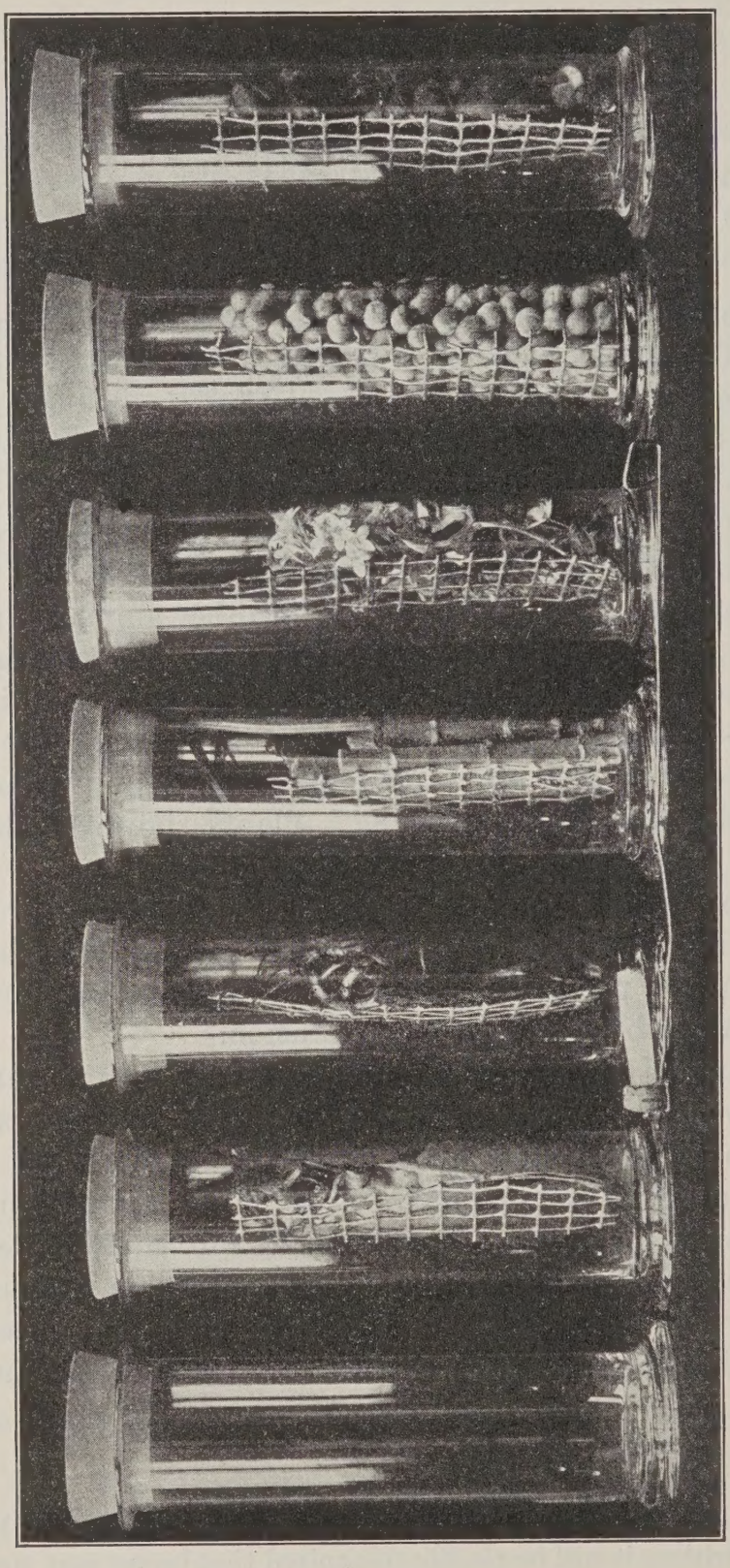


FIG. 93.—Experiment to demonstrate the exchange of gases that accompanies plant-respiration. Explanation in the text.

living roots (washed free from soil but moist and fresh), green leaves, freshly opening flower buds, and (in the last jar) fresh mushrooms or other fleshy fungi. Test the air in the empty half of each jar with a lighted taper to make sure that it contains sufficient oxygen to support combustion, and then seal all the jars air-tight with rubber stoppers, and set them side by side in any convenient place except in direct sunlight.[1] At the end of 12 to 24 hours again test the air in each of the jars with the lighted taper. The air in the first jar, containing no plant material, will still support combustion, but the taper will be extinguished at once when lowered into each of the other six jars.[2] This shows that the air in each of these jars has become poorer in oxygen, and that it does not now contain enough to support combustion.[3] This observation justifies the inference that living plants take in oxygen.

Carbon Dioxide Given Off.—The air in each of the seven cylinders may next be tested with lime-water, by pouring in not more than one or two tablespoonfuls, and mixing it well with the air by tipping the cylinders, holding the halves with the plant material uppermost, and allowing the lime-water to flow back and forth a few times from one end of the jar to the other. Care should be taken not to dirty the lime-water by allowing it to rinse the plant material. After this treatment the lime-water will be found to have turned milky in all of the jars except the one containing no plant tissue. From these results we may correctly infer that carbon dioxide has been given off by the plants.

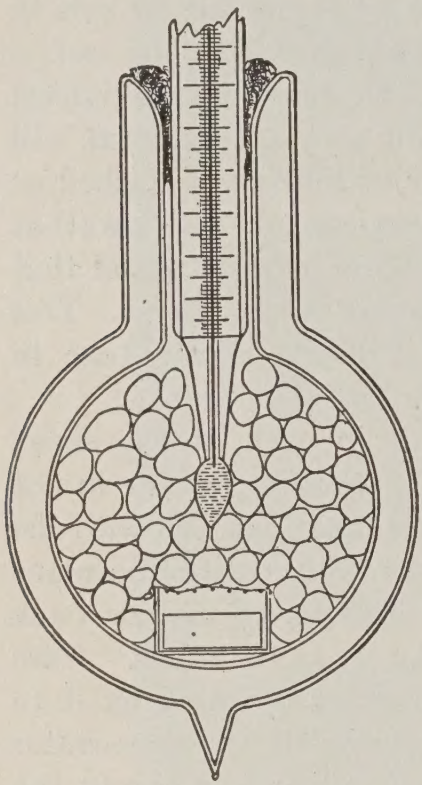
Heat Evolved.—That heat is evolved during the gaseous exchange above demonstrated may be illustrated by placing a delicate thermometer into, say, the germinating seeds. The best

[1] The heat of direct sunlight is unfavorable to the best results.

[2] If the taper is not extinguished in the jar containing the green leaves, the student should be able, from his knowledge of other plant processes, to suggest a probable reason why, and to devise suitable modifications of the experiment so as to demonstrate the respiration of green leaves. *In this and other tests of the air, the cork stopper should not be removed any longer than is absolutely necessary, and the lighted taper should be lowered and removed quickly.*

[3] Does the experiment show that there is *no* oxygen in the jars in which the flame is extinguished?

results will be obtained by placing the plant material into a double-walled Dewar flask (or a thermos bottle), which will retain nearly all of any heat that may be given off (Fig. 94). If the temperature is recorded at the beginning of the experiment, and again at the end, a rise of temperature will be noted. In one experiment, set up with germinating pea seeds (air-dry weight 80 grams) in a Dewar flask as above described, a rise of 19.3° F. was observed within 96 hours.



[Fig. 94.—A simple calorimeter for studying the temperature transformations in respiration. Respiring seeds are placed in the Dewar bulb (double walled, with a vacuum between the walls). At the bottom of the bulb is a dish containing caustic potash; cotton wool is packed between the thermometer and the neck of the bulb. (After Ganong.)

Respiration versus Breathing.—In the case of man and other animals, the exchange of gases and evolution of heat, demonstrated by the experiments described above, are an index of respiration. The process of taking in oxygen and giving off of carbon dioxide by animals is called breathing. It is better to restrict the term breathing to the mechanical exchange of gases between the lungs of animals and the external air, and to confine the term respiration to the oxidation processes of the living protoplasm. It will thus be recognized that *respiration is a function of every living cell*, and that the cells of our fingers, for example, respire just as truly as do those of our lungs and other organs. The lungs, by their mechanical expansion and contraction, merely serve to bring the oxygen of the external air into intimate contact with the blood, which carries it to all respiring tissues of the body. There is no process in plants comparable to this breathing. In the case of some animals without lungs, certain specialized organs (in fishes, the gills) are continually bathed with external oxygen, which passes into the blood *by diffusion*. This more closely resembles the process by which oxygen from the air passes into the plant body. In other animals

(*e.g.*, earthworms) there are no special organs for breathing, and the oxygen diffuses through the moist body-walls.

Stomata and Gaseous Exchange.—In Chapter IV we described the openings or stomata in the epidermis of leaves, through which water-vapor passes to the outside. We shall also learn in Chapter IX that the interchange of gases in photosynthesis takes place through the stomata. So, also, does the exchange of gases that accompanies respiration. As the oxygen within the cells is consumed in respiration, more diffuses in from the intercellular spaces. Thus its pressure becomes less within the leaf than without, and consequently oxygen enters by diffusion through the stomata. At the same time the air in the intercellular spaces becomes richer in carbon dioxide than the air outside, and therefore this gas passes out, also by diffusion.

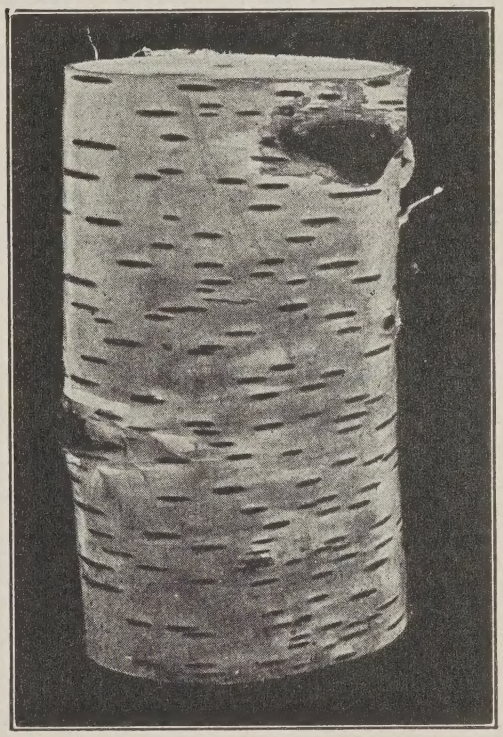


FIG. 95.—White Birch (*Betula populifolia*). Portion of a branch showing the prominent lenticels.

Lenticels.—Many living cells and tissues are more deep-seated than the mesophyll of leaves, and oxygen obtains access to these cells by different ways in different plants. Only one of these cases may be considered here. If any young woody twig is examined, small "dots" or lines will be discovered on the surface. On closer examination these will be found to be small openings through the bark (Fig. 95). They are known, from their shape, as *lenticels* (Latin, *lens*). The outer portion of the bark, and the older, inner layers of wood are not alive, but the cambium layer, between wood and bark, and the cells immediately adjacent, are alive, and therefore need a continual supply of fresh oxygen. This is supplied through the lenticels by gaseous diffusion, in a manner quite analogous to that by which the supply in the leaves is maintained.

Special Organs for Respiration.—Numerous plants have special organs which have been generally interpreted as serving primarily

to facilitate the process of gaseous exchange, particularly in respiration. Such is the commonly accepted interpretation of the "knees" of the swamp cypress (*Taxodium distichum*). As this tree grows in or near the edge of water, the roots must grow in soil that is more or less saturated with water, and, therefore, poorly aerated. They send up into the air vertical branches which seem to have no other function except that of aeration.

Numerous palms have peculiar structures that appear to serve the purpose of aeration. Jost, who first described these structures for the palm, *Livistona australis*, gave them this interpreta-

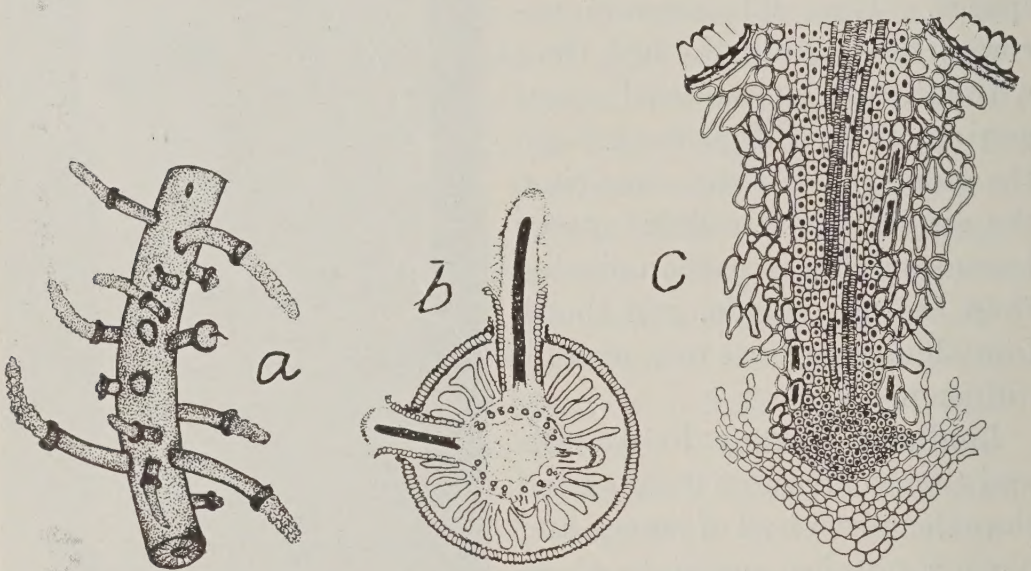


Fig. 96.—Pneumathodes of the Oil Palm (*Elaeis Guineensis*). *a*, Magnified portion of a root showing pneumathodes in various stages; *b*, cross-section through root, showing 4 pneumathodes in longitudinal section at different stages of development; *c*, Longitudinal section through a pneumathode, showing the aerating tissue (greatly magnified). (After Yampolsky.)

tion and called them *pneumathodes*. They are found on other palms (Fig. 96), on the screwpine (*Pandanus*), sugarcane (*Saccharum*), species of Sedge (*Cyperus*), and other plants.

Respiration a Continuous Process.—So long as a plant or animal cell remains alive, respiration never ceases. Cut flowers in the florist's, vegetables stored over winter, fruits and vegetables in transportation and in the market, ensilage in the silo, the roots of perennials in the ground over winter, seeds stored in grain elevators and elsewhere—in fact all living tissues are constantly respiring. The loss of solid matter (carbon) in respiration is often considerable. Kiesselbach and Helm germinated wheat

grains on non-nutritive pure quartz sand, watered only with distilled water and grown in absolute darkness so that no new substance could be formed by photosynthesis. When the seedlings ceased to grow, the parts of the root and shoot were dried and carefully weighed, and also the inert parts of the grain. The sum of these weights subtracted from the moisture-free weight of the original seeds gave the amount of matter that passed off as carbon dioxide in respiration. In this way it was found that the loss of weight during fourteen days of growth amounted to 39.22% of the original moisture-free weight; in other words, over one-third was lost in respiration.

In the case of stored seeds, a condition is reached after a longer or shorter period of time (depending upon the species) which renders further respiration impossible and the seeds die. The seeds are, of course, gradually weakened in their germinating power for some time previous to the time when they may be called dead. Knowledge of these facts helps us to understand why some seeds remain viable longer than others.[1] It also prevents us from giving credence to such stories as appear from time to time in newspapers concerning the germination of wheat said to have lain for two or three thousand years in Egyptian mummy cases. This is a physiological impossibility.

Plant and Animal Respiration.—There is probably no erroneous notion about plants more tenaciously held, nor more widespread, than the belief that plant respiration is the reverse of animal respiration. This error is due entirely to a confusion of the two processes of respiration and photosynthesis. From what has preceded, however, it should now be clear that plants respire

[1] The Japanese botanist, Ichiro Ohga, has recently (Bot. Mag. Tokyo **37**: 87–95. 1923) recorded the discovery, in Manchuria, of seeds of the East Indian Lotus (*Nelumbo nucifera*) buried in peat under a layer of wind-blown soil (*loess*). Evidence justifies the assumption that the seeds are not less than 120 years old, "although it is probable," says Ohga, "that the seeds have remained buried 200 years or even 400 years." All of these seeds which have been tested germinated. Ewart, who tested 2500 kinds of plants in 1908, states that "the probable extreme duration of vitality for any known seeds may be set between 150 and 250 years" (for seeds of the Pea Family—Leguminosae). Ohga's seeds are, then, the oldest viable seeds on record (*Cf.*, p. 110). Delayed germination of seeds in soil results from the fact that their seed-coats are nearly or quite impermeable to water.

in the same way as animals, using up oxygen in the processes of oxidation within their tissues, renewing the supply from the surrounding air (or, in anaerobic respiration, from the breaking down of chemical compounds rich in oxygen), and releasing the carbon dioxide and other waste products resulting from the oxidations. Heat is developed in both plants and animals. The condensation of water-vapor from the breath shows that water is

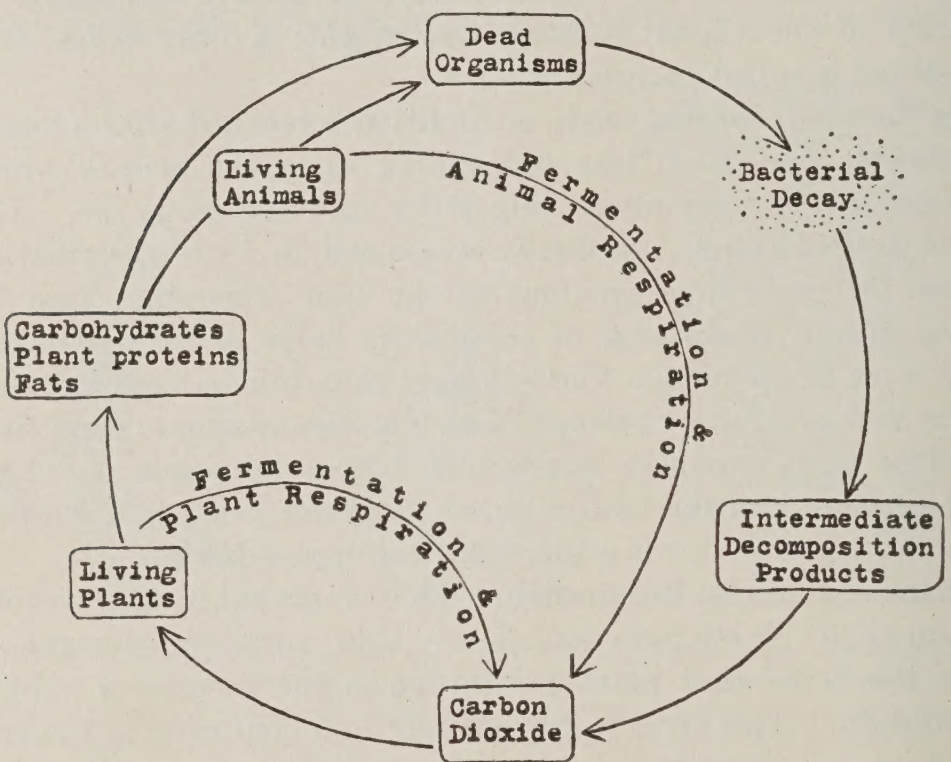


FIG. 97.—The carbon cycle.

formed in animal respiration, and careful, delicate experiments have also shown that water is formed in plant respiration. In both plants and animals respiration converts potential energy (in the form of complex chemical compounds) into kinetic energy —manifest in motion, locomotion, and the overcoming of resistance of various kinds (that is, work). The two processes are compared in the following table:

TABLE III.—COMPARISON OF PLANT AND ANIMAL RESPIRATION

PLANT RESPIRATION	ANIMAL RESPIRATION
1. Oxidations occur within the tissue	1. Ditto
2. Oxygen taken in	2. Ditto
3. Carbon dioxide given off	3. Ditto
4. Heat evolved	4. Ditto
5. Water-vapor formed	5. Ditto
6. Dry weight decreased	6. Ditto
7. Potential energy becomes kinetic	7. Ditto
8. Occurs in every living cell	8. Ditto
9. Occurs without ceasing, day and night	9. Ditto
10. Accomplished by respiratory enzymes	10. Ditto

Respiration and Fermentation.—Perhaps one of the most surprising and interesting of all the results of the study of respiration is the revelation of the fact that *the real process of respiration* (the oxidation of living tissues, as distinguished from the exchange of gases by breathing, or otherwise) is accomplished by enzymes known as oxidases, and *is therefore, in reality, a form of fermentation.* In fact, the more deeply we study all the fundamental processes of living things, the more it seems to become evident that every chemical process in organisms, in fact, that life itself is absolutely dependent upon fermentations. We are brought face to face with the almost startling fact that such commonplace phenomena as the ripening of fruit, the raising of dough, and the decay of plant tissues, are conditioned by the same class of substances (enzymes), and by the same kind of processes that underlie the digestion of food, the respiration of tissues, and the thinking of human minds. And, moreover, we seem to be led to the odd conclusion that *living organisms do not respire because they take in oxygen, but that they take in oxygen because they have respired.*

Effect of Plants on Air in Houses.—There is a wide-spread belief that the presence of plants in living rooms and schoolrooms is deleterious at night because of the carbon dioxide they give off. This belief involves two errors: one, that the main purpose of ventilation is to remove carbon dioxide, and the other that plants give off this gas at night in sufficient quantity to be injurious to health. Recent experiments have clearly demonstrated that ventilation of rooms is needed to keep the temperature and humidity sufficiently low; it also tends (in this way) to prevent

the multiplication of disease-producing germs. But its value does not ordinarily lie in the fact that it removes an excess of carbon dioxide and lets in an abundance of oxygen.[1] Winslow found by experiment that when the air in a room contained 20–60 parts of CO_2 per thousand parts of air (5–15 times the normal amount), the occupants suffered no bad effects, mental or physical, provided the temperature and humidity were not too high. But recent tests by Rigg and others have shown that in a greenhouse well filled with plants growing vigorously in the month of July the air, over a period of fourteen days, never contained more than 3–10 parts per ten thousand of carbon dioxide, or much less than existed in Winslow's experiments. Therefore, there would seem to be little or no foundation in fact for the belief that plants are bad in sick-rooms or other rooms because of the carbon dioxide they give off.

[1] The distressing story of the Black Hole of Calcutta is doubtless responsible in large part for the prevalence of this error. Human beings, of course, cannot live in an atmosphere where the amount of oxygen present falls below a certain percentage, as was the case in the Black Hole. But such conditions rarely, if ever, obtain in buildings inhabited or frequented by men.

CHAPTER IX

NUTRITION

Organic and Inorganic.—All substances belong to either one or the other of two classes of matter—organic or inorganic. Organic substances are, for the most part, those which compose the bodies of animals or plants, past or present, or which have been, or may be, formed by the life-processes of living things. The possibility of synthesizing certain organic compounds (hydrocarbons) artificially in the laboratory has broken down the hard and fast distinction, formerly recognized between organic and inorganic substances. Bone, flesh, shells, bark, wood, leaves, gums, and resins formed by plants; coal, sugar, flour, starch, cellulose, plant and animal juices, and all protoplasm, represent organic substances. Inorganic substances are those which have never been incorporated into the bodies of plants or animals, or if so, have since lost all evidence of that fact. Water, salt, iron, oxygen, carbon, glass, sulphur, air, represent inorganic substances. All chemical elements are inorganic; all organic substances, therefore, are compounds. Sometimes the line is hard to draw. Thus a piece of wood or of bone converted into charcoal, may, if carefully handled, retain unmistakable traces of having formed a part of the body of an animal or a plant, but if the piece is ground in a mortar, a fine powder may result, that has lost all trace of its organic origin. Ordinarily, however, the two kinds of matter are easily distinguished, either by their structure or their known origin. So clearly distinct and unlike are they, that one entire branch of the science of chemistry, organic chemistry, is devoted to a study of organic substances, all of which are compounds of carbon. Inorganic chemistry is concerned with all other substances.

Nutrition of Plants and Animals.—The foods of every living thing—those substances which, by digestion and assimilation, can be incorporated into the structure of the living body as a

part of it—are all organic. In this respect animals and plants are alike; they both require organic substances as food. Thus it is evident that there must be a continual formation of organic compounds out of inorganic in order to maintain the food supply of the world. As we shall soon learn, this is the great and fundamental rôle of green plants in the world's economy—to elaborate organic compounds for food out of inorganic "raw materials." With a very few exceptions among the bacteria, plants that are not green (such as toad-stools, molds, and other fungi), and most

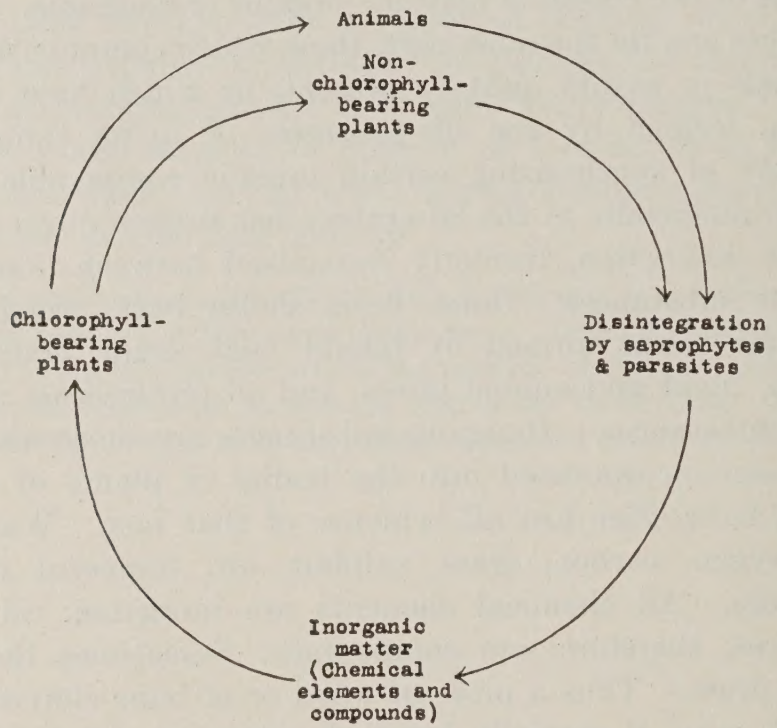


FIG. 98.—The organic cycle.

animals cannot do this. Therefore we are wholly dependent upon green plants for the food supply of the world. Animals and non-green plants live, either directly or indirectly, upon green plants.

The bodies of all living things are constantly giving off inorganic compounds (such, for example, as the carbon dioxide given off in respiration, and the water in transpiration), and after death all bodies are (by the action of bacteria) gradually broken up into inorganic substances. Thus, we see, there is a kind of perpetual cycle, or circulation, from one realm to the other, as indicated in the diagram (Fig. 98).

Kinds of Foods.—When we examine the bodies of plants we find that the foods elaborated are stored in various organs or tissues. These foods all belong to one of three classes of substances, viz.:

Carbohydrates, represented by starch, sugars, and cellulose;

Proteins, represented by protoplasm itself, the gluten of wheat, and other substances;

Fats, represented by the various oils, such, for example, as olive oil and cotton-seed oil.

Chemical Composition of Plant Foods.—A chemical examination of *carbohydrates* reveals the fact that they are composed of the elements, carbon, hydrogen, and oxygen, the two latter occurring in the same proportion as in water, namely, two parts of hydrogen to one of water (H_2O). "Carbon is the central element of organic nature. There is not a living thing, from the minutest microscopic animal to the mammoth, from the moss to the giant tree, which does not contain this element as an essential constituent."

Fats (classed chemically as hydrocarbons) contain the same elements as carbohydrates but in different proportions; while *proteins*, in addition to carbon, oxygen, and hydrogen, always contain nitrogen, commonly sulphur, and often phosphorus.

Essential Elements.—When plant tissue is incinerated, the resulting ash is found to contain the elements calcium, potassium, magnesium, phosphorus, sulphur, iron, and chlorine. All of these substances, except sulphur and chlorine, are metals, and since they are invariably present they are commonly referred to as the *essential elements* of the ash. Carbon, oxygen, hydrogen, and nitrogen must also be included as essential elements.[1] Calcium is not necessary for all fungi (*e.g.*, not for *Aspergillus niger*), nor for all algae. The element sodium (Na), long known to be absolutely necessary for animals (as, for example, in salt, NaCl) was not formerly considered essential for plants. More recent studies,[2] however, disclose the fact that sodium appears

[1] According to investigations of J. S. McHargue (Sci. **56**: 85. 1922), *manganese* is also an essential element "for the normal growth of autotrophic plants." If this is confirmed we must count twelve essential elements, instead of eleven as named above.

[2] Osterhout, W. J. V. Plants which require sodium. Bot. Gaz. **54**: 532–536. 1912.

to be as necessary for some plants as for animals. Thus, for example, various species of marine plants were transferred from sea water to a solution similar to sea water except that the sodium chloride was replaced with other substances (calcium chloride, ammonium chloride, magnesium sulphate, potassium sulphate, and others). "The plants lived much longer in sea water (whether natural or artificial) than in any solution in which the sodium of the sea water was replaced by some other substance." From these and other experiments, Osterhout concludes that one function of sodium is to prevent or antagonize the poisonous or toxic action of the other salts in the solution.

Three main problems now confront us:

1. What is the source of these mineral elements?
2. Where, in the plant, are they elaborated into plant food?
3. How is the process accomplished?

Source of the Mineral Elements.—Since most plants are fixed for life to a certain spot, they must obtain their mineral elements from their immediate surroundings; they cannot, like animals, go in search of them. The hydrogen is obtained chiefly from water (H_2O). The carbon and oxygen are obtained chiefly from the air, where the carbon occurs, in combination with oxygen, as carbon dioxide. Recent experiments of Breazeale on the nutrition of wheat plants show that while these plants do not seem to be able to absorb CO_2 from its solution in water without the presence of a soluble base, still when a soluble base (like sodium nitrate—$NaNO_3$) is present, the roots first absorb the NO_3 as an ion, leaving the sodium which combines with the water and the dissolved CO_2 to form either sodium carbonate (Na_2CO_3) or sodium bicarbonate ($HNaCO_3$). From these dissolved compounds the plants then absorb the CO_3 as an ion. "It seems quite evident that the plant is unable to substitute, to any appreciable extent, the carbon of the CO_3 radical absorbed by the roots for the carbon of the carbon dioxid taken in by the leaves." The experiments suggest "that the carbon needed for building up organic compounds in the plant is derived from the carbon dioxid of the air, and not from the CO_2 taken into the plants through the roots."[1] Free oxygen (as well as oxygen

[1] Breazeale, J. F. The absorption of carbon by the roots of plants. Jour. Agr. Res. **26**: 303–311. Nov. 17, 1923.

in combination with carbon) is also obtained from the air. About four-fifths of the air is nitrogen, and one might naturally infer that the plant could obtain an abundant supply from that source. We shall learn later, however, that most plants can not utilize the free nitrogen of the air, but must have it supplied in chemical combination with other elements, in the form of nitrates. These are obtained from the soil.

Mineral Elements from the Soil.—The calcium, potassium, magnesium, phosphorus, sulphur, sodium, iron, and other elements are also obtained from the soil in the form of soluble salts, such as phosphates, nitrates, sulphates, and carbonates. If a necessary element occurs in the form of a compound not soluble in the soil-water, it may be dissolved by acid (chiefly carbonic acid, H_2CO_3) secreted by roots, or carbonic, nitrous, and various organic acids[1] formed by the activity of soil bacteria, and thus made available. The normal, vigorous growth of plants depends upon the presence in the soil of these so-called *mineral nutrients* in suitable quantities. The relative proportion and the minimum amount of each that is necessary varies with the species or the variety of the plant, the physical condition of the soil (state of cultivation, etc.), rainfall, and other factors. A deficiency in the amount of any one necessary element present in the soil (no matter how abundant the others may be) constitutes a *limiting factor* to the growth of the crop, and in agricultural practice this limitation is commonly overcome by the application of a mineral fertilizer. Ordinarily the soil contains an ample supply of the compounds calcium, magnesium, sulphur, and iron, and only the potassium, nitrogen, and phosphorus compounds have to be supplied by artificial fertilizer. Obviously it is wise to have the soil analyzed before purchasing fertilizer, and then to apply a mixture of known composition, adapted to the needs of the particular case.

The good results of intelligent fertilizing are strikingly illustrated by experiments of Reimer and Tartar[2] in southern Oregon. An analysis of the soil near Tolo, Oregon, indicated an abundance

[1] *E.g.*, Acid of sour milk (*lactic*), of vinegar (*acetic*), of rancid butter (*butyric*), etc.

[2] Reimer, F. C. and H. V. Tartar. Sulfur as a fertilizer for alfalfa in southern Oregon. Oregon Agric. Coll. Exp. Sta. Bull. 163. July, 1919.

of calcium, potassium, and magnesium, a deficiency of phosphorus, and a subsoil very poor in nitrogen and sulphur. Alfalfa had been grown on the field for several years, and the roots of the plants bore an abundance of nodules.[1] The yields had been moderate. In one experiment one plot received "superphosphate" (monocalcium phosphate and calcium sulphate,

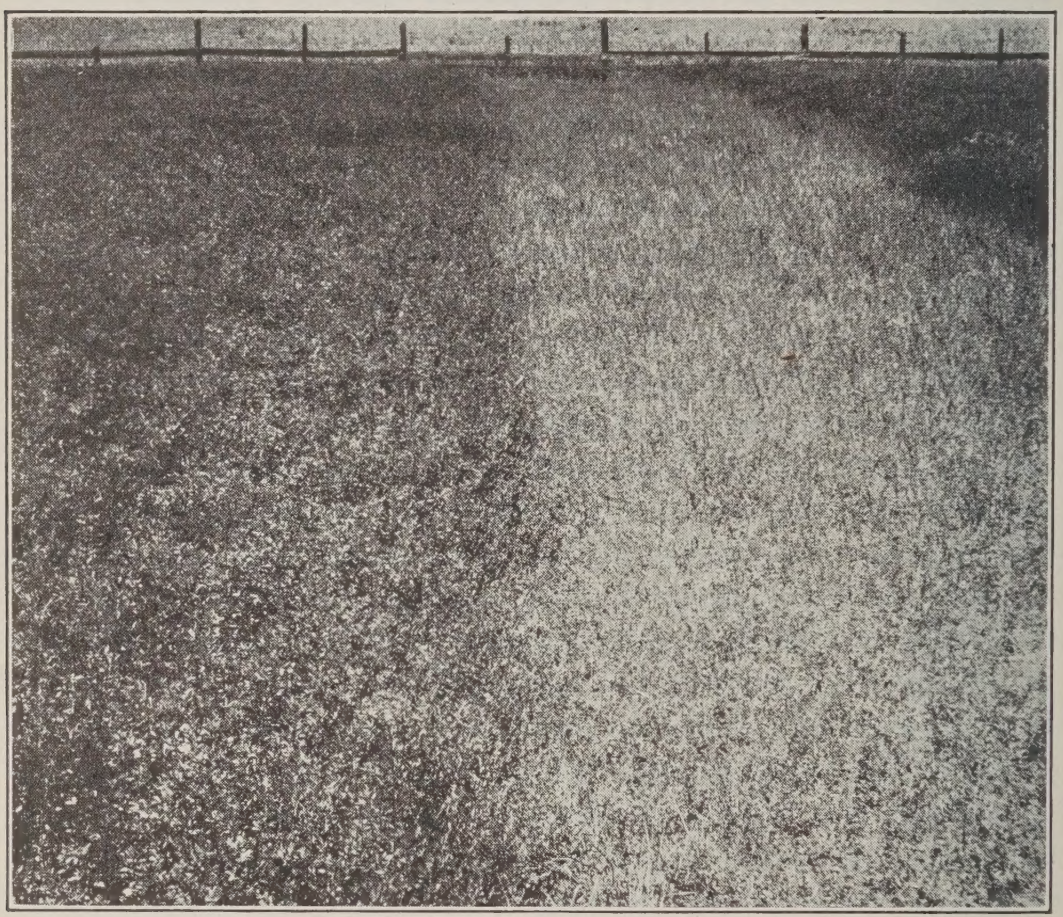


FIG. 99.—Photograph of adjacent plots of alfalfa in a field where it had been growing for several years. The left-hand plot was fertilized with superphosphate, which supplied sulphur at the rate of 100 lbs. per acre. The right hand plot was fertilized with monocalcium phosphate, supplying phosphorus by the same amount as on the first plot, but no sulphur. (After Reimer.)

$Ca(H_2PO_4)_2$ and $CaSO_4$) supplying sulphur at the rate of 100 lbs. per acre, while an adjacent plot was given monocalcium phosphate (supplying phosphorus by the same amount as on the first plot), but no sulphur. The greatly increased yield following the application of the sulphur is strikingly illustrated in figure 99.

[1] See p. 234.

Specific Variation.—There is a wide variation in the mineral needs of various species. This is illustrated by the results of recent studies of the composition of the ash of plants, growing on sand dunes, as compared with the chemical analysis of the sand itself (Table IV).

TABLE IV.[1]—COMPARISON OF MINERAL CONTENTS OF DUNE SAND AND OF THE ASH OF PLANTS GROWING THEREIN

The figures indicate percentages

	Dune Sand	Black Oak (*Quercus coccinea tinctoria*)	Sand Cherry (*Prunus pumila*)	Beard-grass (*Andropogon sp.*)	Scouring Rush (*Equisetum hyemale intermedium*)
Silica (SiO_2)	90.28	32.38	1.50	65.40	49.44
Calcium oxide (CaO)	1.57	28.86	44.13	10.19	13.36
Potassium oxide (K_2O)	1.05	9.51	10.94	6.68	6.01
Magnesium oxide (MgO)	0.73	3.42	4.25	3.21	3.67
Sodium oxide (Na_2O)	2.22	0.82	0.40	4.00	10.37
Aluminum oxide (Al_2O_3)	3.55	0.70	0.02	2.57	2.26
Iron oxide (Fe_2O_3)	1.03	1.50	0.71	2.52	1.04
Phosphoric anhydride (P_2O_5) Trace; less than	0.01	0.91	3.25	2.04	2.55

[1] The data are taken from Richardson, W. D. The ash of dune plants. *Science*, N. S. **51**: 546–551. 1920. This article has been freely drawn on in discussing the data given in the table.

From this table it is seen that, although there was over 90% of silica present, the sand cherry took only 1.50%, while the black oak took over 32% and the *Andropogon* over 65%. The sand cherry absorbed more calcium and much more phosphorus than the oak, but less iron and sodium. Moreover, it should be noted that, while only a trace of phosphorus compound was present (less than 0.01%) the sand cherry appropriated enough to form 3.25% of its ash, and the other plants in equally surprisingly large amounts. The amount of any given substance absorbed by the vegetation does not appear to be determined (or, if so, only slightly) by its concentration in the soil. It might seem as though the plant, as some writers state, would take what it needs, yet in the wood of a dead oak (*Quercus macrocarpa*

Michx.) MacDougal[1] found nearly 500 mg. of metallic copper to each kilogram of dry matter. So far as known, copper does not play any rôle in the normal life processes of the oak; it is very toxic to most plants[2] and, as MacDougal suggests, may have been the real cause of the death of the oak. Like many poisonous substances, copper in very dilute solutions may act as a stimulus to certain life processes. Experiments of Frank and Krüger, for example, indicated that the growth of potatoes was increased by a trace of copper. Mercury, nickel, silver, lead, and other toxic or (so far as known) physiologically inactive substances have been found in the ash of plants. Possibly the correct interpretation is that the materials, and the amount of each, which a plant absorbs from the soil, are controlled chiefly by the structure of the membranes and surfaces through which the materials pass (by osmosis), and not entirely by the *needs* of the plant. Of course, when a plant is storing up large quantities of a substance (such as protein, for example, in beans and other legumes) we would expect it to absorb from the soil and yield in its ash relatively large quantities of the elements that enter into the composition of the stored substance. The fact is that the plant may take in any substance at hand that is in a physical condition to enter by osmosis, and when the net result is favorable the plant thrives, otherwise it becomes sickly or dies.

Plant Injections.—Recent experiments of C. B. Lipton, in California, seem to indicate that certain mineral nutrients, including nitrates, phosphates, and the necessary calcium and magnesium salts, may be supplied to fruit trees by injection into the trunk, thus avoiding complications that may arise from the various chemical reactions that take place in the soil when fertilizers are applied in the usual way. Holes were bored deeply into the trunks of orange and lemon trees suffering from lack of chlorophyll in their leaves (*chlorosis*) and therefore ceasing to

[1] MacDougal, D. T. Copper in plants. Bot. Gaz. **27**: 69–70. Jan., 1899. The Australian plant, *Polycarpaea spirostylis*, is so invariably associated with copper deposits in No. Queensland that it is called the "copper plant," and its occurrence is believed to indicate the presence of copper in the soil.

[2] Copper is specially toxic to green algae and other organisms when used in very dilute solutions; this knowledge has been applied to rid reservoirs and park lakes of an excess of these organisms.

bear. Ferrous sulphate supplied by means of these holes was taken up by the plant, and in three weeks the yellow foliage was replaced by green leaves, and the trees began to show signs of fruiting. Large quantities of these solutions can be absorbed, one pear tree having taken in over 60 quarts of chemicals in 24 hours. Calcium and potassium salts are reported to have a stimulating effect when thus injected. This method of supplying mineral nutrients could, of course, only be supplemental to the normal method.

Do Apple Trees Need Fertilizing?—Experiments carried on at various Agricultural Experiment Stations in the United States, extending in some cases over a period of 25 years, to test the value of applying fertilizers to apple trees, have led to the conclusion that "fertilizers are, in the main, held to be of value on thin or worn out land or in orchards which are making weak growth. At the same time, well-cared-for orchards on good land, under proper methods of clean cultivation and cover cropping, show little favorable response to fertilizer applications."[1]

The long-term experiment of Hedrick and Tukey led them to conclude that in the orchard studied, having well-drained, heavy clay loam, the application of commercial fertilizers has been a waste of both time and money. These investigators suggest that, "in orchards that are run down, or which are making only a few inches of growth, attention should first be given to drainage, cultivation, and general orchard practices, which may be just as effective as the use of commercial fertilizers and far less expensive."[2]

Plant Nutrition an Electrical Phenomenon?—When chemical compounds are dissolved in water the molecules are dissociated or dismembered into component parts called *ions*. Each ion bears an electric charge—some positive, some negative. Thus, when common table salt is dissolved in water, the molecule, NaCl, dissociates into sodium ions bearing a positive electric charge (Na^+), and chlorine ions bearing a negative electric charge (Cl^-). All acid molecules, when dissociated, yield what is known as *hydrogen ion* (H^+), the hydrogen component of the molecule,

[1] Hedrick & Tukey. New York State Agr. Exp. Sta. Bull. 516. Feb., 1924, p. 6.

[2] *l.c.*, p. 21–22.

bearing a positive electric charge. The more dilute the solution the greater the extent to which dissociation takes place.

Soil water is rich in ions that result from the dissociation of the molecules of the dissolved mineral nutrients, and these ions move freely through the soil solution. Recent studies[1] have led to the conclusion that "Plants probably feed upon ions, and these ions probably penetrate the root membrane and move . . . to the tissues as an electric charge; therefore the feeding of plants may be looked upon as an electrical phenomenon."

Root Competition for Nutrients.—We have noted in Chapter VI the struggle between weeds and crop plants for water. There is also a struggle between them for mineral nutrients, for plants vary in their ability to absorb mineral nutrients from soil solution. For example, it has been shown experimentally that, if mustard and oat plants are grown with their roots in the same solution containing only a limited supply of a nitrate, the mustard will absorb it much more rapidly than the oat and will therefore get most of it. In another experiment, when the roots of maize and kafir corn were in competition, the maize got nearly all the nitrates and the kafir corn little or none.

Availability and Fertility.—Since no substance can enter a plant normally except by osmosis, it is evident that the chemical elements which the plant obtains from the soil are not "available" unless they occur in the form of soluble compounds, and are dissolved. A great abundance of food elements occurs in the soil in "non-available" (*i.e.* insoluble) form, and the great problem for modern agriculture is to render them available. This is accomplished chiefly by the geological process known as *weathering*, which includes the chemical and physical action of the atmosphere on rocks and rock-minerals. In this work the chief agents are water and carbon dioxide. As indicated above, certain acid substances (chiefly carbonic acid) secreted by living roots, or given off by dead roots (*e.g.*, fatty acids), or formed by bacterial action, operate to increase the availability of mineral nutrients; further investigation of this subject is necessary.[2] The polished

[1] Brezeale, James F. Nutrition of plants considered as an electrical phenomenon. Jour. Agr. Res. **24**: 54. Apr. 7, 1923.

[2] Liebig (*Ann. d. Chem. u. Pharm.* **105**: 138. 1858) contended that land plants are entirely dependent upon this solvent action of their roots for

surface of a piece of marble placed in contact with growing roots (of a seedling bean or pea, for example) will, in the course of three or four weeks, become etched, so as to show the outline of that part of the root system in contact with the marble.

Various bacteria play an important rôle in this connection by giving off carbon dioxide and thus aiding the process of weathering. It has been stated that the bacteria in the upper 110 centimeters (43 inches) of soil on one hectare (acre and a half) produce several million liters of carbon dioxide each year. The amount of carbon dioxide produced in a soil, and hence its bacterial content, become, therefore, a matter of large importance in determining the availability of chemical elements and thus the fertility of the soil.

The Action of Chemical Infinitesimals.—In addition to the essential elements enumerated above, a dozen or fifteen other elements are found more or less generally in the ash of plants. These include:

Copper.—As noted above, traces of a copper salt have been found to stimulate the growth of potatoes and other plants.

Silicon.—Known to favor the fruiting of oats. Very abundant in the scouring rush or horsetail (*Equisetum*), and in the ash of grasses, rushes, and sedges.

Chlorine.—All plants contain traces, and it has not yet been found possible to grow any plant in the entire absence of chlorine.

Sodium.—Already mentioned on pp. 159–160.

Manganese.—Water-chestnuts (*Trapa natans*) contain 7–14% in their ash. It is present in many other plants.

Aluminum.—Traces occur in most plants.

Iodine and *Bromine.*—Found, not only in sea weeds, but also in land plants.

Fluorine.—Found in barley and peas. According to Solm-Horstmar, the presence of fluorine and lithium is necessary to the full development of summer barley.

Boron, in grapes; *rubidium* and *calcium* in beet roots, *lithium*, *strontium*, *barium*, *zinc*, *cobalt*, *silver*, *vanadium*, and several others.

---

all the constituents of their ash. Experiments since Liebig's time have shown that his conclusion is not correct, since many soils contain the necessary constituents in soluble form; however, this function of roots is of large importance.

The percentage of some of these elements present in the ash is exceedingly small, especially in certain plants. Manganese is usually present in small amount $\left(\frac{1}{1{,}000} - \frac{1}{10{,}000} \text{ of } 1\%\right)$, and Bertrand states that the oxidation and blackening of lacquer by *laccase* requires the presence of minute traces of manganese. In fact, it enters into the composition of *laccase,* which causes the oxidation. It has been shown experimentally that 0.0000375 grain of manganese will increase the growth of the fungus, *Aspergillus niger,* over four times by weight. Even one-tenth of the above amount will stimulate growth.

The influence of traces of boron and aluminum is shown by experiments of Agulhon and of Stoklosa. Agulhon added 25 lbs. of boric acid (= 4.463 lbs. of boron) to a plot of about 27 square feet of garden soil that had lain fallow for several years. Corn was planted on this plot, and on an adjacent one of similar soil, but to which no boron was added. The crops were as follows at the end of seven weeks' growth:

	Plot 1 No boron	Plot 2 Boron
Weight of green corn	8.45 lbs.	13.2 lbs.
Increase in weight	.....	56%
Dry weight	0.98 lbs.	1.48 lbs.
Increase in dry weight	.....	50%

Stoklosa grew beets on two plots of about 1.25 acre each, fertilized by artificial fertilizer, but to one plot he added 4.028 lbs. of aluminum in the form of aluminum sulphate, but added no aluminum to the other plot. The results were as follows:

	Plot 1 No aluminum	Plot 2 Aluminum
Weight of roots gathered per acre	32,310 lbs.	33,915 lbs.
Increase	.....	1,605 lbs.
Weight of leaves	16,425 lbs.	18,565 lbs.
Sugar in roots (percentage)	16.5%	16.7%
Total sugar per acre	5,331 lbs.	5,664 lbs.
Increase in sugar per acre	.....	333 lbs.
Percentage of increase of sugar	.....	6.2%

Elements which produce their effects only in such small traces are referred to by Bertrand[1] as "*chemical infinitesimals.*" Traces of zinc and boron produce similar stimulation. They are present in too small amounts to function as nutrients, but are believed to enter temporarily into the chemical reactions involved in nutrition, and the writer quoted thinks their presence *in minute quantities* is advantageous in all fertilizers. It is seldom necessary to make special provision for this, as they are present as impurities in most of the chemicals employed in the manufacture of fertilizers. In addition to their stimulating action on crop plants, these elements, as well as those which make up the bulk of the fertilizer, affect also the fungi, bacteria, and other microorganisms in the soil, and this, without question, affects the crop plants indirectly. In fact, it seems not unreasonable, as Bertrand has pointed out, that the addition of an element favorable to the growth of some disease-causing fungus may make the crop plants more susceptible to the given disease.

Integration of Chemical Infinitesimals.—The ability of plants to accumulate large quantities of a substance that occurs in very high dilution in the environment is a fact of great theoretical interest as well as of prime physiological importance. The giant kelps of the Pacific accumulate great quantities of *potassium* salts, although potassium occurs in sea water only in the proportion of about 4 parts in 10,000. We are more familiar with the accumulation of carbohydrates and other compounds of *carbon* from the air, which contains only about 3 parts in 10,000. Marine algae may accumulate considerable quantities of *sodium* and *chlorine*, and Oscar Loew found that a given weight of *Elodea canadensis* contained over one thousand times as much chlorine as an equal weight of the water in which it was grown. The relative amount of *iodine* in sea water is so small that scarcely a trace can be detected by chemical analysis (about 2.32 milligrams per 1000 grams, or one liter), yet the ash of certain marine algae contains as much as 0.5 to 2.0% according to the species. Lehman found as much as 30 mg. of copper to each kilogram of dry substance of plants grown in ordinary soil, and as high as

[1] Bertrand, Gabriel. The action of chemical infinitesimals. Revue Scientifique (Revue Rose). Jan. 18, 1913.

560 mg. per kilo in plants grown in rich soils—amounts greatly in excess of the percentage of copper in the soil.

Other Uses of Soil Ingredients.—In addition to their rôle as nutrients and stimulants, the chemical compounds in the soil serve several other purposes.

1. *They May Act as Poisons.*—What is one plant's meat is another plant's poison. Thus, for example, fresh water algae cannot grow in sea water, and marine algae cannot grow in fresh water. Salt-tolerant plants (*halophytes*), which usually occur only in brackish marshes along the sea coast, are found in the region of the salt wells at the southern end of Onondaga Lake, in New York State, under soil conditions not favorable to most inland plants.

2. *They May Have a Protective Action.*—It is now well known that certain substances which may act as poisons are prevented from so acting by the presence of some other substance. Thus, for example, certain plant cells are quickly killed when immersed in a weak solution (0.1 molecular) of common salt (NaCl), but if calcium chloride ($CaCl_2$) is added to the solution in the proportion of one molecule of calcium chloride to 100 molecules of sodium chloride, the cells will remain alive for a long time.[1] In this case it has been shown experimentally that the calcium delays or otherwise interferes with the penetration of the cell-membranes by the sodium. In such cases the two substances are said to be *antagonistic*, and certain experiments indicate that the result is brought about by alteration of the plasma membrane by the antagonistic substance. From such facts we learn that the agricultural value of lime applied to soils depends upon its protective, as well as upon its nutritive or other actions.

The Root-system in Action.—In the following words Richardson[2] has drawn a vivid picture of the activities of the root-system of a plant as it functions to supply the water and dissolved mineral elements from the soil:

"It is interesting to visualize the activities of the growing root tip as it projects itself among the sand grains, moving under the

[1] Osterhout, N. J. V. Some chemical relations of plant and soil. Sci. N. S. **36**: 571–576. 1912.

[2] Science, N. S. **51**: 551. 1920. The original is slightly modified in the above quotation.

reactions of the various tropisms[1] in such wise that the weal of the growing plant is conserved; turning as necessity arises first in one direction, then in the other, but on the whole maintaining its direction; wedging its way molelike underground, expanding, holding fast; neglecting grains of silica, lying close to potash silicates, absorbing chance molecules of calcium bicarbonate and phosphates, furnishing the chemical means if need be, of bringing the insoluble substance it requires into solution; keeping the cell pumps going to furnish the water supply to the plant in time of rain or drought; a very center of ceaseless activity."

[1] See p. 271.

CHAPTER X

FORMATION AND ROLE OF CARBOHYDRATES

Careful and thorough studies have established, beyond all doubt, the fact that, with rare exceptions, the *inorganic food elements are combined to form carbohydrates only in the green cells of plants*—either in leaves, stems, or other parts. This is one of the most fundamental facts in all science. Among those entitled to credit for this discovery may be mentioned Jan

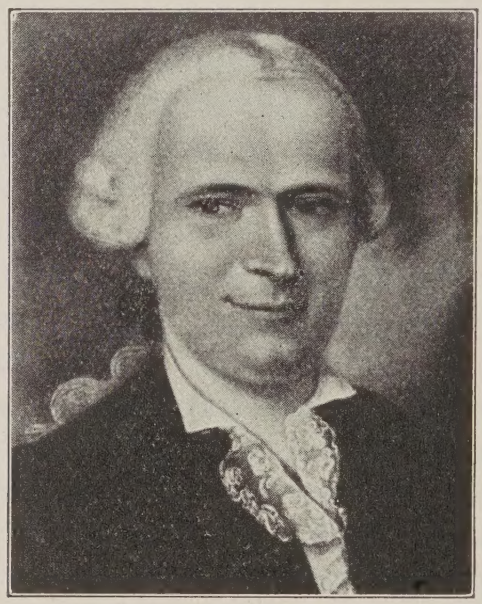


FIG. 100.—Jan Ingen-Housz (1730–1799). He was the first to recognize the difference between photosynthesis and respiration in plants.

Ingen-Housz (1730–1799), a Dutch physician; and Jean Senebier (1742–1809) and Nicolas Theodore de Saussure (1767–1845), two Frenchmen. Joseph Priestley, an Englishman, also contributed to this work, both directly and indirectly, by his discovery, in 1774, of the gas oxygen, and his experiments on the "purification" of the air by green plants.

Van Helmont's Experiment.—Long before the investigators of the 18th century studied experimentally the question of

plant nutrition, Van Helmont[1] performed one of the first (if not the first) recorded quantitative experiments in plant physiology. Aristotle had taught that the food of plants was elaborated in the soil and supplied to them in solution in water, but Van Helmont believed that the plant manufactured the food in its own body out of the water which it absorbed. His experiment was made to prove the correctness of this hypothesis.[2] The experiment consisted in growing a willow, weighing five pounds, in dry soil weighing (when "dry") 200 pounds. The tree was allowed to grow for five years, during which time nothing was added but water. At the end of this period both the tree and the dried soil were carefully weighed. The tree was found to weigh 169 pounds, but the soil, when dried again, was found to have lost only two ounces. Van Helmont interpreted this result as proving his hypothesis that all the tissues of a grown plant are formed chiefly from water. The conclusion was, of course, erroneous, and, judged by modern standards, the experiment was crude,[3] but the introduction of the quantitative method in plant physiology was a long stride forward.

[1] Johannes Baptiste Van Helmont (1577–1644), a Flemish scientist, educated at the University of Louvain. With Paracelsus (about 1490–1541), he was one of the founders of physiological chemistry. In one of his experiments he incinerated 69 pounds of oak carbon. After the carbon had been consumed there remained only one pound of ashes. Van Helmont concluded that 68 pounds of carbon had been converted into invisible air which he called the gas (spirit) of the wood; it was the gas which today we call carbon dioxide. This appears to be the first recorded use of the word "gas." It was Van Helmont who discovered that carbon dioxide turns lime water milky. In one of his books he declares: "I have seen and handled the philosopher's stone" (supposed to be able to transmute baser metals into gold). He was the last of the alchemists.

[2] This, of course, is a violation of scientific method. In the search for truth (research), experiments should not be made for the purpose of *proving* the correctness of a hypothesis (this would imply that the experimenter took for granted the very thing to be proved); they should be made for the purpose of testing the correctness of the hypothesis. The experimenter should be open-minded until all the evidence is in, and evidence *against* the hypothesis should be as welcome as evidence for it.

[3] We are not told, for example, whether any account was taken of the weight of the leaves formed and shed each year during the experiment. The weighing, however, carefully done for those days, was undoubtedly extremely crude, judged in the light of modern laboratory standards for quantitative work.

That so gifted a scientist, and especially the one who first recognized the existence of carbon dioxide (his "gas sylvestre"), and that the atmosphere is composed of a mixture of different gases, should have so completely missed the teaching of his classic experiment shows how easy it is to draw wrong conclusions from our observations. The incident also emphasizes by what slow, painful steps the knowledge we possess has been obtained, and how greatly we are daily indebted to our scientific predecessors. If Van Helmont had possessed the chemical knowledge now the common heritage of high school students, he could

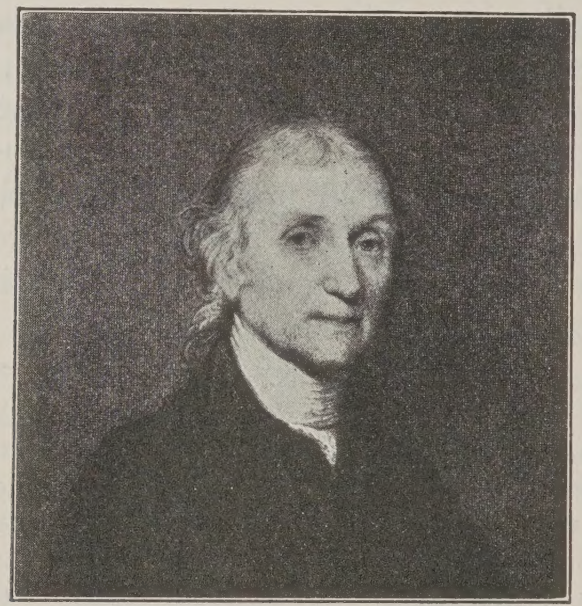


FIG. 101.—Joseph Priestley (1733–1804). He discovered oxygen, and made pioneer studies of the function of chlorophyll.

hardly have failed so completely to interpret correctly the results of his work. It will be instructive for the student to analyze this experiment in the light of what he knows as to the nature and sources of the materials that enter a plant and contribute to the formation of its tissue.

The Significance of Leaves.—In order to understand the point which Van Helmont missed, we must first understand the structure and functions of green leaves for, while the formation of carbohydrate food may take place in any cell containing the green substance, chlorophyll (leaf-green), the chief organs for this work are the leaves. This explains many facts about leaves—*e.g.*,

why they are green, why they are thin and usually broad, why they are often much larger in young, rapidly growing plants that need much nourishment, than in mature plants (Fig. 102), why they occur at or very near the tips of the branches, where they are well exposed to light (Figs. 103 and 104). *There is no more important fact in botany, nor indeed in all natural science, than that all the food of the world is primarily manufactured in*

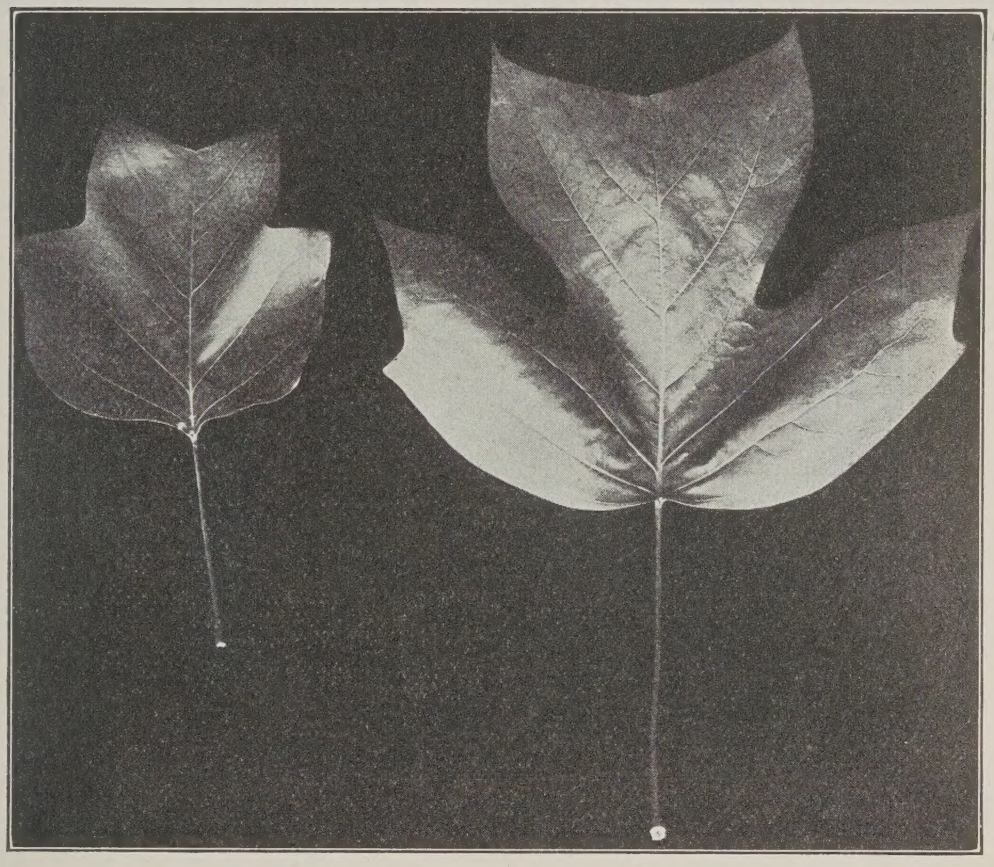


FIG. 102.—Leaves of the tulip tree (*Liriodendron tulipifera*). At left, from a large mature tree; at right, from a young sapling. Average sized leaves were chosen from each tree. Greatly reduced.

the chlorophyll-containing cells of plants. By some botanists the term *chlorenchyma* is used to designate any tissue composed wholly of chlorophyll-containing cells.

Source of Carbon Dioxide.—In the preceding chapter reference was made to the fact that the carbon required by plants is obtained almost, if not quite, wholly from the air, where it occurs in the small proportion of about three parts by volume and approximately two parts in 10,000 by weight. Small as the

quantity is, it is sufficient to meet the needs of the vegetation of the earth, and the supply is continually being renewed by the respiration of animals, the burning of fires, and in other ways.

Numerous experiments have been made to ascertain whether plants would be benefited if they were grown in an atmosphere artificially made richer in carbon-dioxide. Cummings and Jones[1] grew plants of various kinds in open cases into which carbon dioxide, generated continuously, was slowly liberated. By diffusion the gas became distributed throughout the interior of the cases and the leaves of the plants were thus bathed in an

FIG. 103.—A tree (hornbeam), seen from "outside," showing the dense foliage at or near the tips of the branches. The same tree as in figure 104.

atmosphere much richer in carbon dioxide than ordinary air. The percentage of carbon dioxide varied in the different experiments, and could be controlled at will. The best amount also varied with the kind of plant. The plants experimented with included beans, peas, radishes, potatoes, chard, endive, lettuce, strawberries, cyclamen, and others. It was found that, in general, excessive carbon dioxide in the air stimulates plant growth and increases the total crop, acting in a manner similar to fertilizer applied to the soil. The chemical composition of

[1] Cummings, M. B. & C. H. Jones. The aerial fertilization of plants with carbon dioxid. Vermont Agr. Exp. Sta. Bull. 211. May, 1918.

the plants does not appear to be greatly changed by the excess of carbon dioxide in the air, although they showed a very slightly higher percentage of carbohydrates.

Importance of Sunlight.—Plants and plant parts grown in the dark are, with rare exceptions, never green. This means that sunlight is necessary in order to make chlorophyll. But green plants cannot elaborate food in the dark. This means that sunlight is necessary, not alone for the formation of chlorophyll, but for food making as well.

FIG. 104.—A tree (hornbeam), seen from among the branches (as the squirrel sees it), showing absence of leaves except at or near the tips of the branches. The same tree as in figure 103.

It has been found by Harvey and others that electric light from a nitrogen-filled tungsten-filament lamp may be substituted for sunlight in growing plants. Harvey, using lamps of 200 watt and 1000 watt strength, found that plants, exposed to no other light whatever, grew well, and set good seed or produced tubers. The plants were exposed continuously, with no alternation of light and darkness, and it was found that under such conditions the elaborated carbohydrates were translocated, showing that darkness is not essential to translocation. The plants used included a number of cereal grains, potatoes, toma-

toes, squash, peas, cabbage, buckwheat, and others. These results may have more than a scientific interest, for artificial light might be used without great expense, in growing crops in high latitudes where the days are short and the sunlight of low intensity.

Non-green tissues, even in sunlight, cannot manufacture food; for this process both chlorophyll and sunlight are necessary. The green cell has often been likened to a factory; the chlorophyll is the machinery, the sunlight is the energy, while the product of the factory is the manufactured food.

Details of the Process.—The manufacture of carbohydrates involves three essential steps:

1. Taking in the raw materials (water and carbon dioxide).
2. Recombining these parts into carbohydrates.
3. Giving off the waste material (oxygen).

Taking in the Raw Materials.—We have seen in Chapter IV that the air spaces between the green cells of a leaf are in direct connection with the outside air through the stomata. In the presence of sunlight the formation of carbohydrates begins in the green cells. This uses up the carbon dioxide in the cells, and the supply is renewed from the intercellular spaces. The gas, dissolved in water, passes through the cell-walls and the layer of protoplasm. This results in reducing the amount (and thus the pressure) of this gas in the intercellular spaces, and, as a result, more carbon dioxide passes by diffusion through the stomata to the intercellular spaces. Thus, as fast as the gas is used the supply is renewed from without.

Photosynthesis.—Within the cell, the carbon dioxide and water (or simple combinations of these) are finally, *by a series of steps,* recombined by the chlorophyll or green substance found in the chloroplasts (p. 16), into a carbohydrate—probably some form of sugar. This action takes place only in the presence of sunlight. *It is this series of steps that is called photosynthesis.*[1] Not all of the oxygen, contained in the water (H_2O) and carbon dioxide (CO_2) used, enters into the composition of the carbo-

[1] The word means combining (*synthesis*) in the presence of, or by means of, light (*photos*). Whether the first sugar formed in photosynthesis is sucrose or glucose (grape sugar), or whether in some plants it is one and in other plants another form of sugar, is not as yet definitely determined.

hydrate. The unused portion is set free, and is either utilized in other processes, or diffuses out through the stomata to the surrounding air. Thus, the taking in of carbon dioxide and the giving off of oxygen are outward indications that photosynthesis is going on inside the green cells.

Apparatus for Studying Gaseous Exchange in Photosynthesis.—Although photosynthesis and the taking in and giving off of the gases used and produced thereby are two distinct processes, a quantitative study of the exchange of gases affords a basis for calculating the amount and the rate of photosynthesis. Many pieces of apparatus have been devised for this purpose. One of the simpler is that of Osterhout,[1] described by him as follows: "The apparatus consists of a large tube (a lamp chimney will serve) closed at the bottom by a stopper through which passes a tube (*A*, Fig. 105) of Pyrex glass. Through the stopper at the upper end passes the neck of an atomizer bulb (*B*) with an opening at *C* for the intake of air. To the neck of the bulb is attached a tube of Pyrex glass which extends to within an inch of the bottom of the tube *A*.

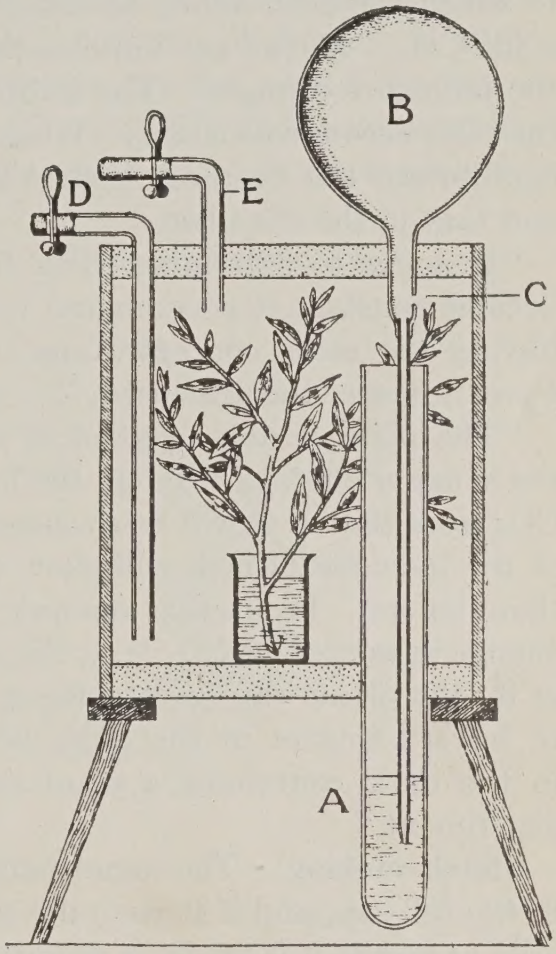


FIG. 105.—Apparatus for measurement of amount and rate of photosynthesis and respiration. Explanation in the text. (After Osterhout.)

"Plants[2] are placed in the chamber with their stems dipping in water contained in a small beaker. By means of the tubes *D*

[1] Osterhout, W. J. V. Apparatus for the study of photosynthesis and respiration. *Bot. Gaz.* **68**: 60–62. July, 1919.

[2] *Tradescantia* may be recommended for this purpose, especially kinds without stripes on the leaves.

and *E* any desired amount of CO_2 may be run into the chamber. When this is finished the bulb is repeatedly squeezed so as to force the gases in the chamber to bubble through the liquid contained in the tube *A*. This liquid consists of distilled water, to which has been added an indicator which is sensitive to (the acid) CO_2. As the gas bubbles through the liquid the color of the indicator changes. The bubbling must be continued until the color becomes constant. When this is achieved we know that equilibrium has been established between the CO_2 in the liquid and that in the chamber.

"In order to determine when the color of the indicator has become constant it is compared with a series of buffer solutions having the same concentration of indicator and contained in Pyrex tubes of the same size.

"The plant is now exposed to sunlight. After exposure the gas is again bubbled through the liquid. If the plant has taken CO_2 from the air it will be evidenced by the change in the color of the indicator, which will show a greater degree of alkalinity than before. From the amount of change in alkalinity the change in tension of CO_2 (*e.g.*, the amount which has been taken in by the plant) can be calculated . . . It is always advisable to have a control in the light without a plant and a control in the dark containing a plant similar to the one used in the experiment."

Starch-making.—The sugar made by photosynthesis is soluble in the cell-sap, and if it were not removed from the solution, at least as fast as it is made, it would accumulate and thus interfere with the manufacture of more sugar. Some of it is removed at once, either by nourishing the protoplasm of the cell where it was formed, or by being *translocated* to other parts of the plant. But some of the sugar is removed *from solution* by being converted into starch, a substance not soluble in water. Thus the accumulation of starch in a leaf or other green tissue indicates that photosynthesis is in progress, and that the resulting carbohydrate is or has been formed faster than translocated. It has been estimated that less than 1% of the energy of sunlight is utilized in starch-making by photosynthesis. The remaining 99% is used to heat the tissue, evaporate water from it, make chlorophyll, and in other ways, while some of the sun's energy is lost,

so far as physiological processes are concerned, by being reflected, and by passing through the plant tissue.

The Steps in Starch-formation.—For a long time it has been recognized that the conversion of sugar to starch depends upon the presence within the cell of certain bodies or plastids known as *amyloplasts* (starch-forming bodies), illustrated in figures 106 and 11. While the amyloplasts are the seat of this process, it is now known (as noted in Chapter VII) that the process itself (a complex one, consisting of several steps) is accomplished by

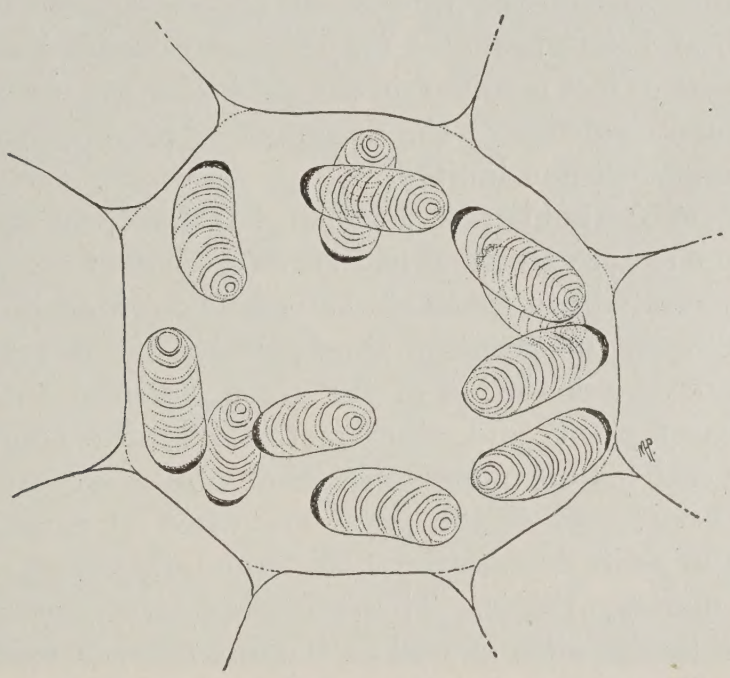


FIG. 106.—Cell of *Pellionia Daveauana*, showing starch-grains. The black, crescent-shaped body on the end of each grain is the *amyloplast*. Greatly enlarged. (Cf. Figs. 11 and 108.)

enzymes. It is probable that a series of enzyme actions is involved in photosynthesis. Careful experiments have suggested that the *first* step in the formation of starch may be the interaction, in the presence of light, of water and carbon dioxide, under the agency of an *oxidase*, resulting eventually in formaldehyde (CHOH).[1] The subsequent steps may be something as follows:

[1] According to Prof. E. C. C. Baly (*Nature* **110**: 856. Dec. 23, 1922) the formation of formaldehyde in the leaf probably takes the following course:

1. Chlorophyll A + H_2CO_3 + light = Chlorophyll B + CHOH.
2. Chlorophyll B + Carotin = Chlorophyll A + Xanthophyll.
3. Xanthophyll + light = Carotin + Oxygen.

2. Condensation of the formaldehyde molecules into a simple sugar, dextrose ($C_6H_{12}O_6$), by *aldehydase*.

3. Transformation of dextrose into a more complex sugar, maltose, by *maltase*.

4. The changing of maltose into dextrine by *dextrinase*.

5. The conversion of dextrin into soluble starch (amylum) by *amylase*.

6. The conversion of soluble starch into insoluble starch by yet another ferment or enzyme, *coagulase*.

Other analyses of the process of photosynthesis have been suggested, and it is probable that the one outlined above may become more or less modified in the light of future investigations. In fact, our knowledge of the dynamics of photosynthesis is, at present, imperfect and limited.

Amount of Carbohydrate Formed.—It has been ascertained that for one square meter of leaf surface one-half a gram to one gram of carbohydrate (*photosynthate*) is elaborated in one hour, depending upon the duration and intensity of the sunlight, the temperature, the condition of the green tissue as to turgidity, the species of plant, and other factors. In the course of one season several billion pounds of carbohydrate are produced by photosynthesis. All of the grain harvested in a season is, of course, so far as its dry matter is concerned, the direct or indirect result of photosynthesis. This process has a direct practical bearing on the quality, as well as the quantity, of various plant products. Thus, for example, studies of Caldwell,[1] extending over a period of five years (1919–1923,) have shown that the content of sugar, acid, and astringent substances present in the juices of fully ripened grapes is determined very largely, if not altogether, by the number of days of sunshine occurring between March 1 and September 30. The year of maximum sunshine was the year of maximum or next-to-maximum sugar content and of minimum acid and total astringency content of the grape juice.

Correlation between Photosynthesis and Leaf Symmetry.—In portions of the leaves of the flowering maples (*Abutilon* sp.)

[1] Caldwell, Joseph S. Some effects of seasonal conditions on the chemical composition of American grape juices. Jour. Agr. Res. **30**: 1133–1176. June 15, 1925.

the chlorophyll is often lacking. In *Abutilon savitzii* the chlorophyll is commonly absent from the marginal region. Absence of chlorophyll from the tissue means, of course, that photosynthesis cannot take place there, and the tissue is hence dependent upon the adjacent green tissue for its carbohydrate food and is not as well nourished as the green tissue. When the chlorophylless tissue is more or less symmetrically arranged around the margin the leaf is correspondingly symmetrical, but when the white

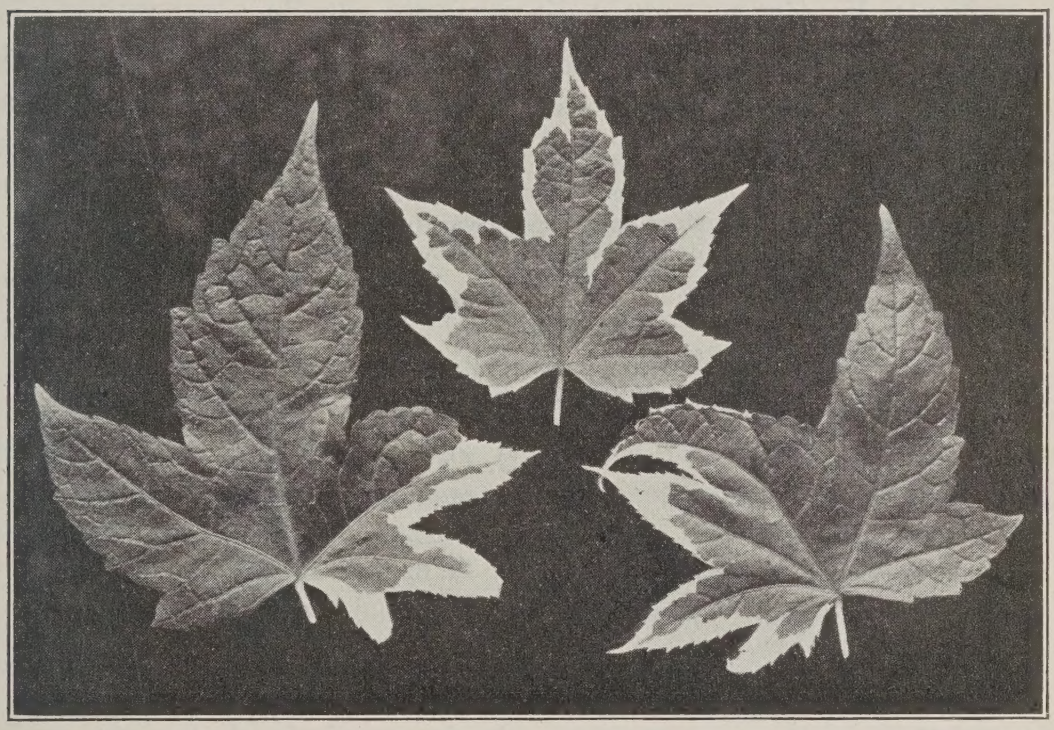


FIG. 107.—Leaves of a flowering maple (*Abutilon savitzii*), showing correlation between photosynthesis and leaf-symmetry.

tissue is asymmetrically disposed the leaf is correspondingly asymmetrical (Fig. 107).

Respiration and Photosynthesis.—The two processes of respiration and photosynthesis are often confused, but in reality they have very little in common, except that both result in an exchange of gases with the external air. But it must be kept clearly in mind that the processes themselves are quite distinct from the exchanges of gases that accompany them, or result because of them. Photosynthesis furnishes carbon to the plant in a form available for use; respiration is the physiological process by which the carbon is utilized to supply the energy necessary for all life-

processes. The result of the two processes is the continual income and outgo of carbon. The carbon enters and leaves the plant in the same form, namely carbon dioxide. The disintegration of carbohydrates is also accomplished by bacterial decay and other fermentative processes. We thus see that there is a continuous circulation of carbon in nature, known as the *carbon cycle* (Fig. 97). A comparison between the two processes is shown in Table V.

TABLE V.—COMPARISON OF RESPIRATION AND PHOTOSYNTHESIS

1. **Photosynthesis** Changes inorganic matter into plant-foods (carbohydrates), which are **Assimilated** and used by the plant	To supply energy for **work,** To repair waste **(Nutrition),** In the construction of new parts **(Development),** including **Reproduction.**	All of these processes are dependent upon **Oxidation** within the cells. This process of oxidation is called	2. **Respiration,** which involves The taking in of oxygen, The oxidizing of oxidizable matter, The release of all products of these oxidations.

PHOTOSYNTHESIS	RESPIRATION
1. Takes place only in cells containing chlorophyll.	1. Takes place in all active cells.
2. Requires light.	2. Can proceed in darkness.
3. CO_2 absorbed, O set free.	3. O absorbed, CO_2 set free.
4. Carbohydrates formed.	4. Carbohydrates consumed.
5. Plant gains in dry weight.	5. Plant loses in dry weight.
6. Kinetic energy of sunlight becomes potential energy.	6. Potential energy becomes kinetic energy.

Chemosynthesis.—In the first paragraph of this chapter it was stated that, *with rare exceptions*, the inorganic food elements are combined to form carbohydrates only in the green cells of plants. Among these exceptions may be mentioned the "sulphur-bacteria" (*e.g.*, species of *Beggiatoa*), wholly without chlorophyll or other pigment. These organisms appear to be able to synthesize organic compounds from inorganic substances in the absence to light. Since 1887 botanists have generally accepted Winogradsky's theory[1] that they obtain their energy for this by oxidizing sulphuretted hydrogen (H_2S), the reaction being expressed by the formula

$$2H_2S + O_2 = 2H_2O + S_2$$

This process is called *chemosynthesis* (in contrast to photosynthesis). Recent studies by Becking have led to the conclusion that

[1] Winogradsky. Bot. Zeit. **45**: 488. 1887.

some other substance like hydrosulphide ion (HS^-) or sulphide ion (S^{--}), more probably the former, is the source of the energy.[1]

In a somewhat similar manner some of the so-called "iron-bacteria" (species of several genera of filamentous bacteria) obtain their energy by oxidizing ferrous to ferric compounds of iron—*e.g.*, by precipitating ferric hydrate from a solution of ferrous carbonate. These bacteria have probably been agents in the formation of deposits of bog-iron.

Manufacture of Proteins.—Proteins are formed *de novo* only in living plant cells, by combining the products of photosynthesis with the nitrogen and other elements supplied in the form of nitrates and other salts. Their formation may be favored by light but, unlike the process of photosynthesis, protein-formation does not require either light or chlorophyll. The formation of proteins occurs in large measure in foliage-leaves, but may take place in any living cell. The manner of their formation is not as well understood as is that of carbohydrates.[2]

Fats.—Fats may occur in plant cells in either liquid or solid form. We are most familiar with the liquid fats, such as the various oils derived from plants. Fat occurs in the solid form in the cocoanut. In the tallow-tree (*Sapium sebiferum*) it is so abundant, as a waxy coating on the seeds, that it is used in eastern Asia for making candles. Fats commonly occur in droplets in the protoplasm, or as an emulsion in the cell-sap, but the place and method of their formation have never been fully determined.

Translocation of Food.—Just as the water and mineral nutrients taken in by the roots must pass up through the stem to the leaves to be manufactured into plant-foods (carbohydrates, proteins, fats), so also must the elaborated plant food pass from the leaves to the branches, main stem, and roots in order to nourish the latter. We have seen in Chapter V that if a tree is girdled in the spring the leaves will remain fresh until autumn,

[1] Becking, L. B., Proc. Soc. Exp. Biol. Med. **22**: 127–129. Nov., 1924.

[2] Recent studies by Gurjar, with tomato, turnip, and radish plants, show that the supply of nitrogen determines the relative proportion of carbohydrates and proteins in the plant. Tomato plants, *e.g.*, will not fruit except when the C:N ratio lies between 4 and 6. Photosynthesis was found to vary inversely as the C:N ratio. (*Science*, N. S. **51**: 351–352. Apr. 2, 1920.)

and this is evidence that the "ascending sap" passes up through the wood. But most trees, when girdled, will seldom live more than one season, for the roots, and all stem parts below the girdling, die of starvation. From this and other evidence we know that the food elaborated in the leaves passes down through the inner tissues or phloem of the bark, being utilized on the way to nourish the cambium between the bark and the wood, the axillary and other buds, the flowers and forming fruit, and the roots.

Is There a Lateral Transfer of Foods, Water, and Mineral Nutrients?—"Are the mineral nutrients and water absorbed by the roots on one side of a plant translocated to and used by the trunk, branches and leaves on that side only, or are the mineral nutrients and water transferred easily through or around the trunk to all parts of the trunk, branches and leaves? Conversely, is the food manufactured on one side of a plant translocated equally to all parts of the plant or does it remain, more or less, in the same side of the plant in which it was synthesized? Are the roots on one side of a plant dependent for their organic matter on the limbs and leaves directly above them? In other words, does a woody plant act as a unit as regards the intake and utilization of mineral nutrients and water, and the synthesis, translocation, and storage of foods, or do individual parts or sections of the plant function independently in these respects?"

These questions are raised by Auchter[1] at the beginning of his paper giving the results of his experimental investigation of these problems. Auchter experimented with young peach and apple trees, privet bushes, privet cuttings, and young oak trees. In one experiment nitrate of soda was applied on the ground under four-year-old peach trees as follows. Three trees were used for each form of treatment.

a. Check. No nitrate of soda applied.

b. Nitrate of soda applied evenly on the ground under the spread of all the limbs.

c. Nitrate of soda applied on the ground under the spread of the limbs on one side only.

[1] Auchter, E. C. Is there normally a cross transfer of foods, water and mineral nutrients in woody plants? Univ. Maryland. Agr. Exp. Sta. Bull. 257. Sept., 1923.

d. All of the roots on one half of each of three trees were carefully cut off close to the trunk. Nitrate of soda was then applied evenly under the spread of all the limbs.

e. All of the foliage on one half of each of three trees was removed and kept removed throughout the experiment.

We have given here only a partial report of the experiment. The experiment was started in June, and one month later observations and tests were made of the amount of nitrates in the foliage of the various trees, of the amount of growth in thickness of the stem, and the amount of food stored. The evidence obtained by these experiments and also by experiments of other investigators appears to "show quite conclusively that the mineral nutrients absorbed by the roots on one side of a plant are in a large measure translocated to and used by the trunk, limbs and leaves directly above them. There is apparently very little cross transfer in a plant."

We have all seen trees with spirally twisted trunks, and it has been found that in such trees the nutrients taken in on one side of the tree may be carried to the branches on the opposite side, for the vascular system follows the twist in the wood of the trunk.

The evidence obtained by Auchter also indicates that the foods elaborated in the leaves on one side of a plant are used and stored chiefly on that side and reach the roots only directly beneath. Experiments of Proebsting (cited by Auchter) also show that, if the leaves are removed from one half of an apple tree, the branches on that side cease to increase in diameter, although the undefoliated branches continue their normal increase in diameter. This showed that the defoliated branches got none of the nourishment elaborated by the leaves on the opposite side.

The evidence as to the transfer of water from one side to the other of a tree was not conclusive, but suggests that water may pass around the plant. If this should prove to be the case we should have to conclude that the mineral nutrients may move independently of the so-called "transpiration current."

The knowledge obtained by these and similar experiments is not only of scientific interest, as enabling us more fully to understand a plant, but it may have practical importance in orcharding.

We must at least recognize that it does make a difference whether one cultivates or applies nitrate fertilizer between every two rows of trees, or only between every alternate two rows.

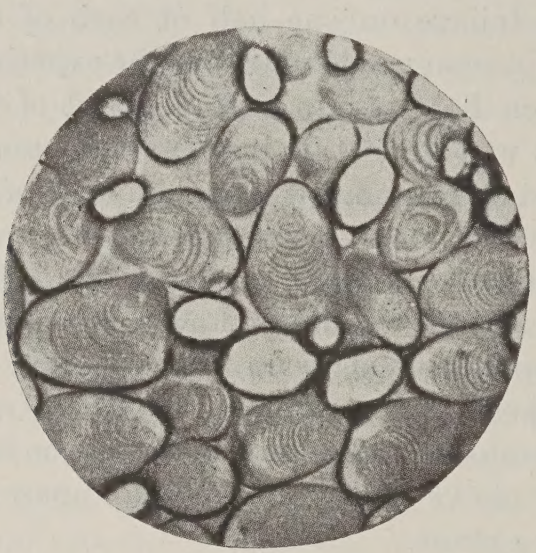


FIG. 108.—Starch grains from a potato tuber. (After Duncan J. Reid.)

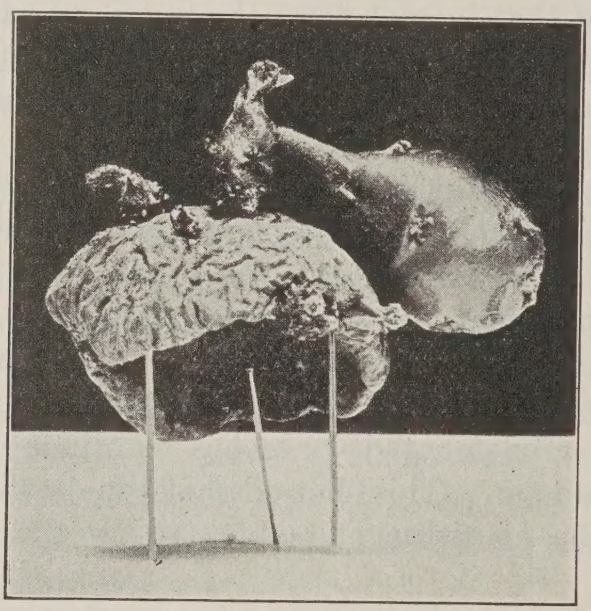


FIG. 109.—Young potato tuber, developed (in light) as a branch of a sprout of an old seed-tuber. Part of the food elaborated and digested in the leaves of the parent plant was translocated down the leaf-stalk and stem, and stored in the older tuber, part of which is shown in the figure. After this piece was cut off, the stored food began to be digested and translocated to the developing "eye" or bud, accompanied by the development of the latter into the young tuber. Ordinarily such changes, in the potato, occur only underground and in the dark.

Storage of Food.—Often the elaborated food accumulates faster than needed. This is what always occurs in certain

parts of the plant, such, for example, as the tubers (underground stems) of potatoes (Figs. 108 and 109), the roots of turnips, the seeds of beans, peanuts, and other plants, the fruits of all plants, the leaf-base of the onion (forming the scaly bulbs or "onions"), and all buds when they are forming. In these *storage organs* part of the soluble sugar is removed from solution by being converted into starch or other insoluble substances, and the storage organs and tissues finally become filled with an excess of food.

The world is dependent for most of its food (for its most important foods) upon this storage habit of plants, but it should be kept in mind that the food is not stored for the use of man, but for the use of the plant itself; it is a method of tiding the plant over periods of "famine," quite as much as is the storage of nuts in the fall by squirrels, or the canning and dessication of fruits and vegetables by man. Any organ may be utilized, on occasion, for storage; the method varies with the species, the environment, and the habit of life.

In annual plants the period of "famine" is encountered only by the embryo in the seed; in such plants, therefore, we find the storage of food confined to the seed. It may be in the embryo itself or around it, or both. In beans, peas, lupines, apples, and related fruits, sunflower, most nuts, and many other plants, reserve food is stored in the embryo, which is thus fleshy, and occupies all the space within the seed coat (Fig. 157). In other seeds, such as the castor oil (*Ricinus*), *Nux vomica*, pepper, and others, the food is stored around the embryo in the form known as *endosperm*, or *perisperm*, or both,[1] while in such seeds as corn (*Zea Mays*) and many of the smaller grains, the food is stored partly in the embryo and partly or largely in the endosperm that surrounds it (Fig. 111). When the embryo resumes its growth in the "germination" of the seed it has neither roots to absorb water and mineral salts from the soil, nor green leaves to elaborate food by photosynthesis; it is therefore wholly dependent upon the elaborated food with which it is either gorged or in contact in the seed.

[1] Endosperm is either female gametophyte tissue, as in gymnosperms, or the product of the fertilization of the endosperm nucleus, as in angiosperms; perisperm belongs to the (sporophytic) nucellar tissue of the ovule (megasporangium). The distinction cannot be understood unless one understands the morphology and physiology of seed formation. See Chapter XVI.

In the case of plants that require more than one season to mature seed (*perennials* or *biennials*) a larger reserve supply is needed to meet the early spring demands of a larger amount of tissue about to resume growth, and stems, roots, and leaves are all utilized, as indicated in the preceding paragraph.

Perhaps the most common food stored in plants is starch, as, for example in potato, corn, rice, wheat, oats. The disappearance of sugar from sweet corn during storage is due chiefly to

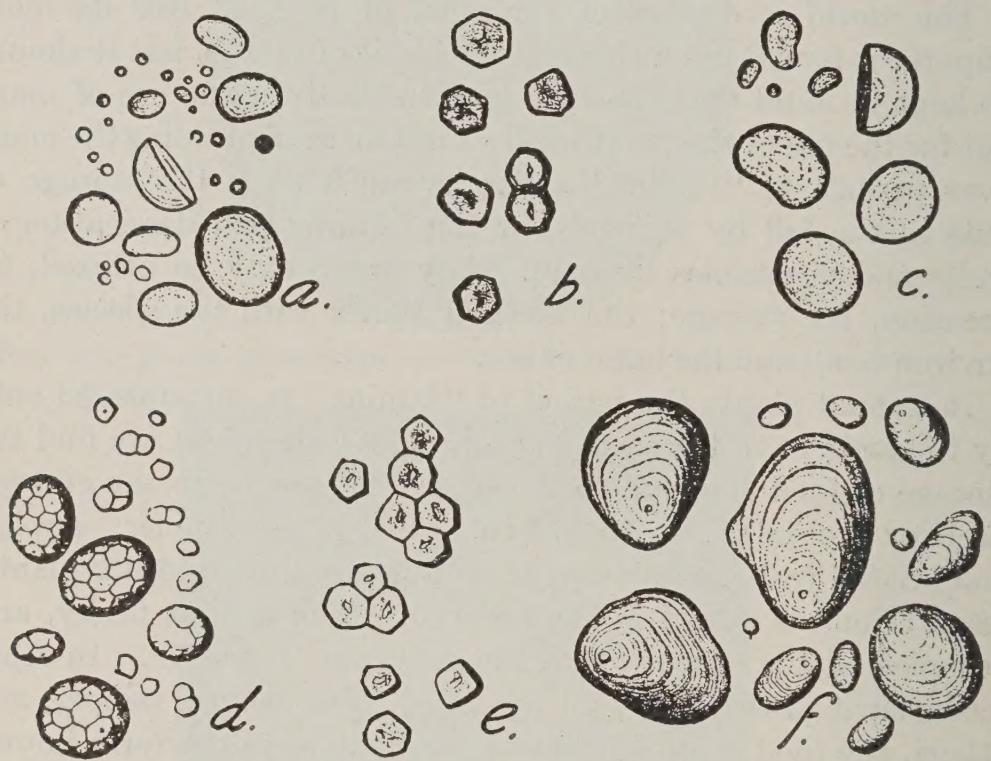


FIG. 110.—Forms of starch grains. *a*, wheat; *b*, Indian corn; *c*, barley; *d*, oats; *e*, rice; *f*, potato. (After Goodale.)

its conversion into starch, and this accounts (in part) for the wrinkling of the dried grains.[1] The reserve food in onions is chiefly dextrose, in the snowdrop (*Galanthus nivalis*) it is chiefly glucose, sucrose, and d-fructose, (maltose and starch being absent); in certain fruits it is levulose, in sugar cane, turnips. sugar beets, and other forms it is cane sugar (saccharose). Saccharose cannot be utilized by most plants until it is converted

[1] Some of the loss of sugar is due to respiration. According to Appleman and Arthur (Jour. Agr. Research **17**: 137–152. July 15, 1919), "One ton of husked green sweet corn during the first 24 hours of storage at 30° C. would lose approximately 3.2 pounds of sugar on account of respiration."

by enzymes (digested) into dextrose or levulose. This process takes place in the sugar cane when it is flowering, and in the sugar beet when it is allowed to complete its life-cycle and come to seed.

Starch is usually stored in the form of starch grains, and the shape, markings, or structure of these grains is characteristic for each species (Fig. 110). From this fact it is possible, by a microscopical examination of starch or the powdered parts of plants,

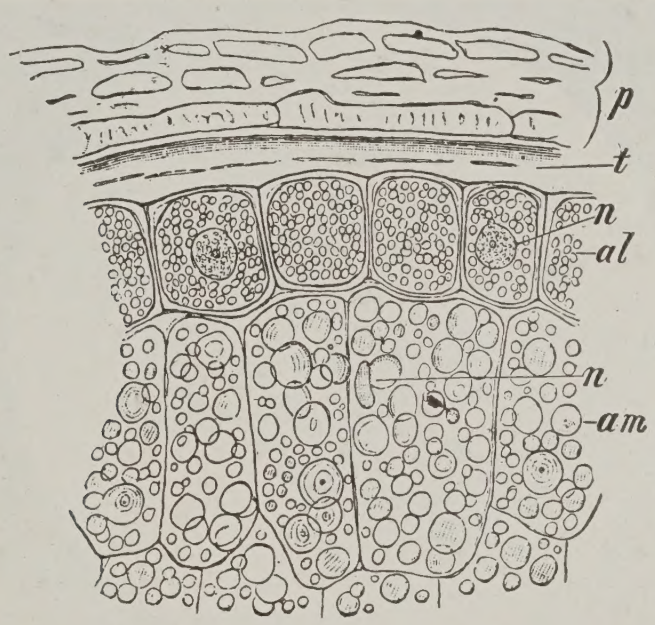


FIG. 111.—Section through the outer portion of a grain of barley. *p*, pericarp of the fruit; *t*, testa of seed; *al*, layer of cells containing aleurone grains; *am*, cells of the endosperm, containing starch-grains; *n*, cell-nucleus. (After Strasburger, from Reynolds Green.)

to identify the kind of plant from which it came, and this is of value in determining the purity of drugs, and detecting the extent and kind of adulteration.

In date seeds, the seed of the vegetable-ivory palm, and other plants, food is stored in the form of cellulose; in the Jerusalem artichoke as *inulin;* in cotton and flax seed and many nuts as oil or fat. The underground stems (rhizomes and tubers) of many plants have an abundance of nitrogenous substances—glutamine, asparagine, and others—in their cell-sap, and these are often rich in stored protein, commonly in the form of *aleurone*

grains (Fig. 111).[1] Because of this fact, nuts and other seeds are often substituted for lean meat to make up a balanced diet.

It will be recognized at once that materials stored by the plant to provide for its own needs not only supply the most staple articles of man's diet, but are consequently the basis of some of our largest industries. In fact, agriculture itself, the basic industry of mankind, consists fundamentally in raising *en masse* (as crops) plants that store up food in large quantity, and in

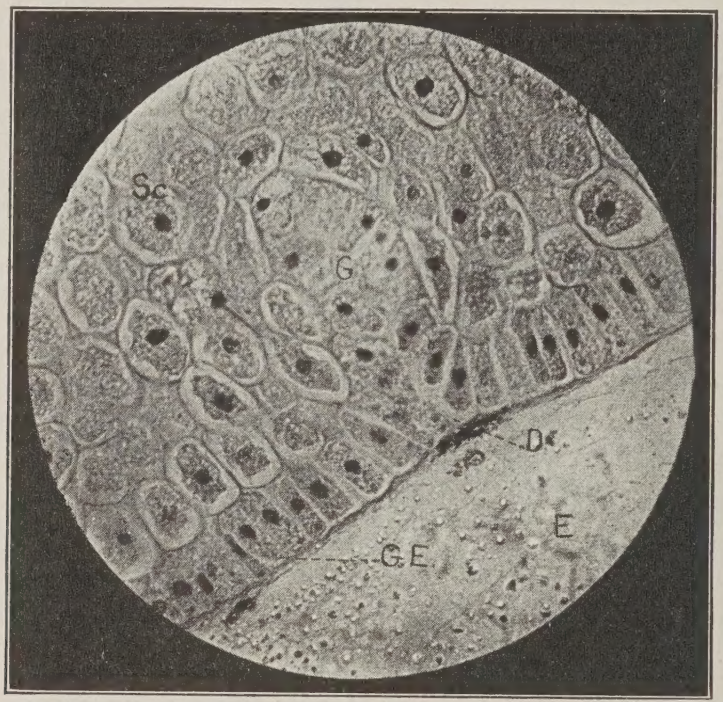


FIG. 112.—Portion of a cross-section of a grain of Indian corn (*Zea Mays*). *G.E.*, glandular epithelium of the scutellum which secretes diastase; *G*, a simple racemose gland in the tissue of the scutellum; *D*, duct of the latter, emptying into the starchy endosperm surrounding the embryo.

harvesting and marketing and utilizing for livestock, the plant-organs or parts in which the food is stored.

Digestion.—We have learned above (Chapter III) that substances can enter a plant only in solution. It is also true that substances, even when inside the cell, cannot be utilized as food by the plant unless they are in solution. In order that the

[1] It is interesting to note that, although the Greek word *aleuron* (ἄλευρον) means *wheaten flour*, modern wheat flour (except "whole wheat") has had the aleurone removed.

protoplasm can be nourished, therefore, all insoluble stored foods must be converted into soluble substances and dissolved. *The process of converting an insoluble food into a soluble substance and*

FIG. 113.—Venus's flytrap (*Dionaea muscipula*). Insects are captured by the rapid closing together of the two valves of the leaf-blade. When the valves come together the rigid marginal teeth interlock, making escape impossible. The digestive enzyme is secreted by glands distributed over the inner surface of the valves. (After John Ellis.)

dissolving it is digestion. This change, like the various processes in photosynthesis, is brought about by various *enzymes*, which have the power of converting insoluble starch, proteins, and fats, into soluble substances.

Digestive enzymes are probably secreted by every active plant-cell. In the corn grain the cornstarch (endosperm), surrounding the embryo, is digested during germination by diastase secreted by a glandular epithelium of the embryo. Often

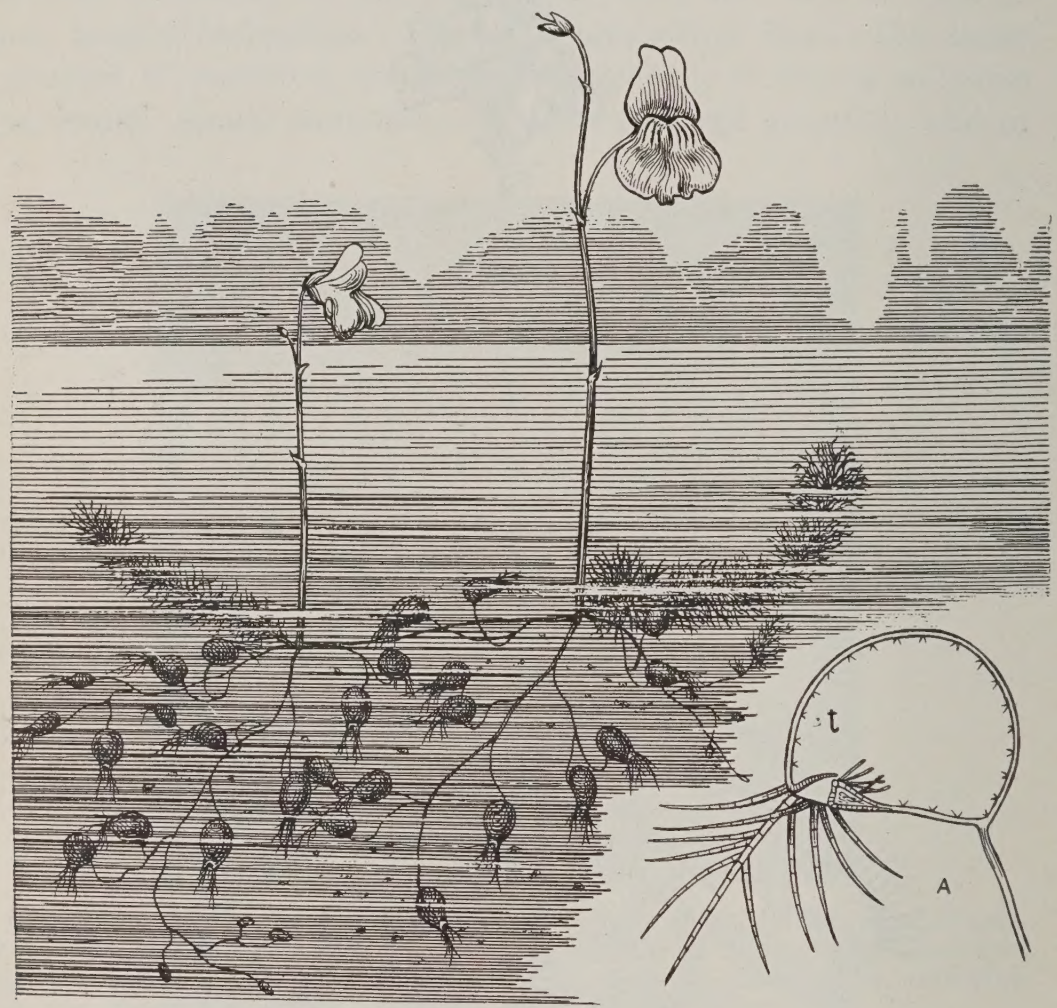


FIG. 114.—An aquatic insectivorous plant called Bladderwort (*Utricularia Grafiana*). The submerged stems bear small bladder-like organs which have been interpreted as modified leaves. Small animalcules become entrapped in these bladders where they are digested and absorbed as nourishment by the plant. In the lower right-hand corner one of the bladder-like leaves of another species (*Utricularia neglecta*) is shown in section. The entrance to the bladder is protected by numerous hairs, and by a trap-door (*t*). (Drawing based upon Kerner.)

this glandular layer is invaginated, so as to form a true gland (Fig. 112).

Insectivorous Plants.—A special case of plant nutrition is presented by the insectivorous plants, of which there are many

kinds. They are all characterized by the possession of some device for capturing insects that visit them, and by the ability to secrete a proteolytic enzyme capable of digesting the protein tissues of their prey. These plants can also digest any meat fed to them artificially. After being digested, the protein food is absorbed by osmosis. The Venus's flytrap (*Dionaea muscipula*), numerous species of bladderwort (*Utricularia*), and several species of sundew (*Drosera*) serve to illustrate the insectivorous plants (Figs. 113–115). Although these plants are able to digest protein, experiments have shown that a protein diet is not necessary either for their life or healthy growth.

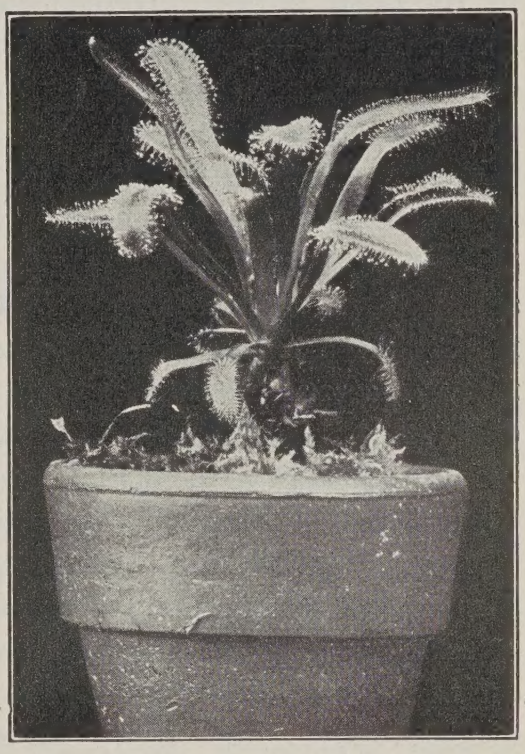


FIG. 115.—A sundew (*Drosera intermedia*), showing the glandular tipped tentacles on the leaves. When an insect alights on a leaf he is held by the sticky secretion; the tentacles then bend over in contact with his body, holding him more firmly, and pouring out a protein-digesting enzyme secreted by their glands.

Assimilation.—After food has been elaborated and digested it still is not a part of the living protoplasm, but only lies within the vacuoles of the protoplast. It is no more a part of the plant than is food in our hands or stomachs a part of our bodies. One step more is necessary; the digested food must be incorporated into, and made part of, the living protoplasm itself. It must be transformed from lifeless matter into living matter. As in the case of enzyme action, the process by which this remarkable change is brought about is not understood. By multitudes of accurate, painstaking experiments, however, one great fundamental truth has been estabished, namely, that non-living matter can be converted into living matter only by the action of other living matter already existing. Proteins, sugars, and fats have all been manufactured from simpler substances, artificially in the laboratory, without the aid of living organisms; and they may all

be digested artificially in a test-tube, also without the aid of living organisms; but, although the attempt has often been made, no one has ever succeeded in artificially producing even the minutest drop of living protoplasm. So far as we now know, only living protoplasm, acting directly on non-living matter, can bring about that marvellous change. This fact is concisely expressed by the Latin phrase, "*Omne vivum e vivo*" (All life from life).

Biogenesis.—That living matter is *always* descended from preceding living matter, and that it *never* arises spontaneously from the non-living is the principle of *biogenesis.*[1] Opposed to this principle is the principle of abiogenesis,[2] which teaches that living matter may originate from non-living without the intervention of other living matter. This was formerly quite generally believed. Men thought, for example, that putrid meat might become transformed directly into the maggots (young flies) so often found in it; but we now know that maggots in decaying meat always arise from the eggs of flies that have previously visited the meat and deposited their eggs there. Thanks to the painstaking experiments and clear thinking of Redi, Pasteur, Tyndall, and others, belief in the principle of biogenesis is now practically universal among scientists.

That living matter could not, under favorable conditions, originate from non-living matter, or that it did not in the beginning, or never does now, cannot, of course, be demonstrated; one can never, experimentally or otherwise, prove a universal negative. The principle of biogenesis affirms that, in experiments conducted with the utmost skill, and with every possible precaution to exclude all traces of living matter, no faintest manifestation of life has ever been detected; we therefore logically conclude that, however life may have been *originally* created, it never originates now from non-living matter, but always from living matter only.

Dissimilation.—Nothing is more unstable than protoplasm. No sooner is new protoplasm formed by the process of assimilation than it begins to disintegrate, forming various new sub-

[1] Biogenesis, from the Greek words *bios* (βίος), life, and *genesis* (γένεσις) generation.

[2] Abiogenesis. The prefix *a* (Greek *alpha*) deprives the remainder of the word of its meaning, or reverses the meaning.

stances, such as cell-walls, gums, resins, latex, coloring matters (in flowers and other plant parts), the perfumes of flowers, the poisons of poisonous plants, and the substances that give the various flavors and tastes to different kinds of plants. The process by which all such substances are formed by protoplasm is called *secretion.* Thus we see that *protoplasm is in a state of continual formation and disintegration.* The sum total of all these changes, both constructive and destructive, is called *metabolism. It is metabolism, above everything else, that distinguishes living from non-living matter.* We also see that death is essential to life; unless protoplasm perishes no new protoplasm can be formed. All life, it is true, comes from life; but only on the condition that that which is already living shall perish.

Economic Value of Plant Secretions.—Many of the substances secreted by protoplasm are commercial products. This is notably true of wood, all of which consists of lignified cell-walls; of cork, which consists of suberized cell-walls; of the various gums, such as gum arabic, gum mastic, and gum tragacanth; of the resins; and of turpentine, rubber, vegetable dye-stuffs, perfumes, and various other articles of commerce. Other plant secretions may play an important rôle in practical agriculture, in connection with the rotation of crops, and through harmful excretions by roots.

Agricultural Mutilations and Nutrition.—Numerous agricultural practices result in the mutilation of perennial plants, and some of these mutilations are so extensive that they must profoundly interfere with the normal course of nutrition. Howard[1] has called attention to this, mentioning such practices as the cutting of green fodder, the picking of tea leaves, the pricking of the poppy capsule, the grafting and budding of fruit trees, root-pruning, the grazing of young wheat, and the reaping of such fodders as alfalfa. In the latter case nearly the entire shoot-system of the plant is removed when growth and all nutritive processes are at their height. As Howard states, this operation must produce a profound disturbance in the metabolism of the plant. All supply of carbohydrates is suddenly cut off

[1] Howard, Gabrielle L. C. The role of plant physiology in agriculture. Jour. Bd. of Agr. British Guiana. **18**: 113–127. Apr., 1925. Reprinted from Agr. Jour. India. vol. **18**, part III.

from the root-system while it is still left intact and actively absorbing water and salts from the soil, and therefore in need of sustained nutrition.

Crop-plants are apparently able to withstand such a shock in most cases, but the root system is, in some cases at least, profoundly affected. Howard found in the case of indigo (*Indigofera*), which is treated similarly to alfalfa, that a few days after the tops have been cropped at least half the root-system and all the leguminous tubercles (Cf. p. 234) have been killed. The plant then slowly reproduces its root-system and afterward makes new shoots. Very young plants with thin stems, when cropped, are unable to regenerate the lost parts, and consequently die. Since so many agricultural practices are really mutilations, it would be desirable to have more knowledge of this subject; such information might lead to improvements in horticultural and agricultural practice.

CHAPTER XI

SAPROPHYTISM AND SYMBIOSIS

All Food Organic.—In more ways than one it is true that life is dependent upon antecedent life. An illustration of this principle is seen in the case of nutrition, for, with rare exceptions, no living thing, neither plant nor animal, can utilize directly as food the unaltered inorganic elements and compounds derived from the air and soil. This was shown in Chapter IX. While plants are commonly said to obtain their food from the air and soil, strictly speaking this is not true. Carbon, oxygen, hydrogen, phosphates, nitrates, sulphates, *et cetera* are no more plant food than are flour, water, sugar, and salt bread. Just as the elements composing bread would, if eaten separately, make a very unsavory and poor diet, so the inorganic elements and compounds, as such, would not be able at all to nourish plants. They must first be broken down (if compounds), and then recombined into the organic compounds of carbohydrates, proteins, and fats.

Necessity for Chlorophyll.—As we have seen in Chapter X. this recombination of inorganic chemical elements into organic compounds is the function of chlorophyll. Thus it is that, with such exceptions as the iron and the sulphur bacteria (p. 184), green plants are absolutely essential to all higher forms of plant and animal life, and this explains why non-green plants are found only in intimate association, either with living green plants or with the organic remains or products of other living things—plants or animals. Not being able to manufacture their own food, they must find it ready made.

SAPROPHYTISM

Decay.—Perhaps the simplest case of the nutrition of non-green plants is the absorption of food from the organic remains of other plants or of animals, and from animal excrement. When

the spores or other reproductive bodies of such plants begin to grow upon such a substratum, they secrete various enzymes which begin to disintegrate it, reducing it to simpler, soluble substances. This is the process commonly known as "decay," and the plants which cause it are called *saprophytes.*[1] The word "decay" is derived from a Latin word, *decidere,* which means to fall apart, in allusion to the fact that the decaying substance is being disintegrated or broken down into simpler substances, which are recombined by assimilation, in the cells of the sapro-

FIG. 116.—Indian pipe (*Monotropa uniflora*), a saprophyte. (Photo by Elsie M. Kittredge.)

phyte, into protoplasm like its own. Such a state of existence is called *saprophytism.*

Fungous and Bacterial Saprophytes.—Among the more familiar saprophytic plants may be mentioned the common breadmold, the fungi that are instrumental in ripening cheese, the so-called "mildews," which often grow on old moist pieces of leather, and numerous other filamentous fungi; the bacteria which cause the decay of meat and other substances; bacteria which cause the retting of flax stems, thus freeing the bast fibers from which linen

[1] Saprophyte, from the Greek σαπρός (*sapros*), rotten, + φυτόν (*phyton*), plant; a plant growing on decaying matter.

is made by causing the decay or rotting away of the remainder of the tissue; the bacteria which convert cabbage leaves into sauerkraut, the numerous slime-molds (Myxomycetes), and various other forms, which are more or less intimately connected with human industries, or with public or private hygiene.

Humus, one of the most important compounds of soil, is composed almost entirely of the remains of plant and animal bodies in various stages of disintegration, and the disintegration is caused, almost entirely, by the action of enzymes secreted by bacterial

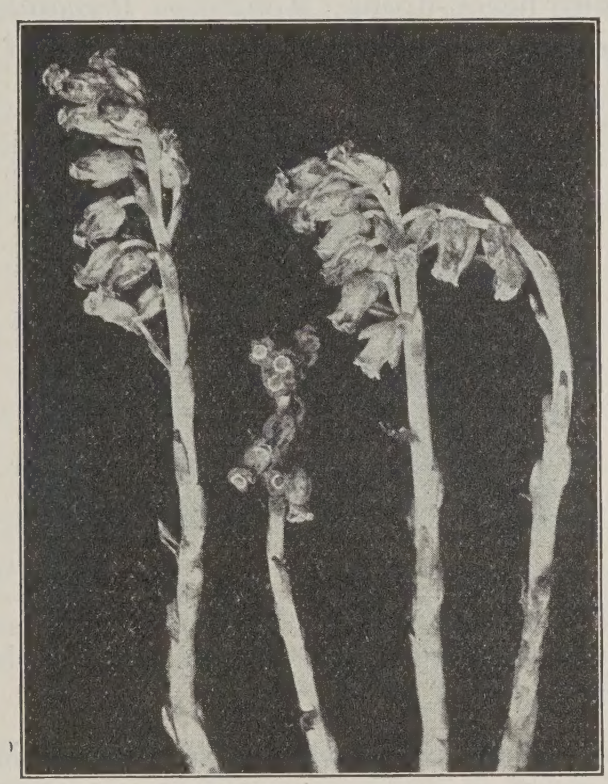


FIG. 117.—False beech drops (*Monotropa Hypopitys*), a saprophyte. (Photo by Elsie M. Kittredge.)

and fungal saprophytes. When the environment is acid, as is usually the case when plant tissue is decaying, fungi are the active agents in the disintegration of organic remains; when the environment is alkaline, bacteria (*e.g.*, butyric acid bacteria and others) are the cause of the disintegration. The annual fall of leaves from deciduous trees, and the plant substance returned to the soil by annual plants, the root-systems of crops, the fall of twigs, branches, and bud-scales, and other parts, and by the entire plant body of dead trees, and otherwise, add enormous

quantities of cellulose and lignin to the soil each year. If this material were not decomposed, not only would the surface of the earth be covered with a thick layer of cellulose, but the growth of crop-plants and of natural vegetation would be impossible through the lack of humus in the soil. Thus we come to realize that these saprophytic plants are absolutely essential to the most fundamental of all human occupations, namely, agriculture.

Saprophytic Flowering Plants.—Not all saprophytes are fungi. The Indian-pipe (*Monotropa uniflora*, Fig. 116), and its close relative, the false beech-drops (*Monotropa Hypopitys*, Fig. 117), are examples of flowering plants, wholly devoid of chlorophyll,

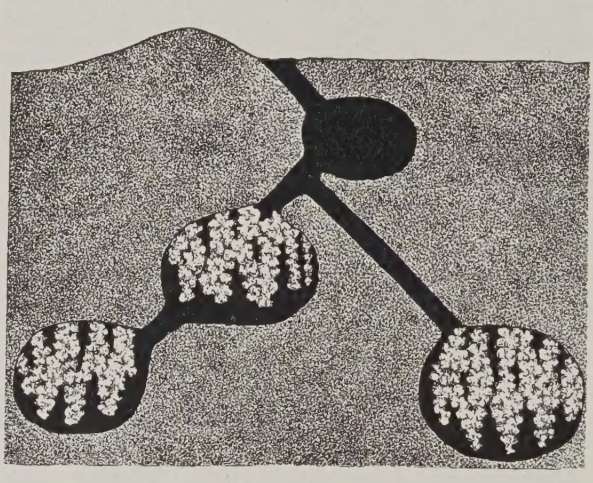


FIG. 118.—Diagram of a nest of a fungus-growing ant (*Trachymyrmex obscurior*), showing four chambers. The pendent white masses in three of the chambers are the mycelium of the fungus—the so-called "fungus-gardens." The species of the fungus has not been definitely determined, but it is thought to belong to the Ascomycetes. (After W. M. Wheeler.)

and therefore unable to manufacture their food, which is absorbed entirely from the humus in which they grow. Other examples are *Lathraea*, and the coral-root (*Corallorhiza*).

SYMBIOSIS

Different Kinds of Symbiosis.—The absorption of nourishment from one living organism by another involves, of course, the intimate association of the two organisms. Two organisms or groups of organisms may also occur normally in close association for other than nutritional reasons. Such a vital association is called *Symbiosis* (living together), and we find organisms living together in all degrees of intimacy and independence, or of interdependence. The two or more organisms may maintain a

loose, disjunctive, or *social symbiosis*, which may be either (1) *non-nutritive*, as when, for example, staminate and pistillate plants of the same species grow together or near each other; or (2) *nutritive*, as in those cases where ants maintain fungus-farms, where they cultivate filamentous fungi for food. Again one plant may merely grow upon another, but without deriving any nourishment from it (*epiphytism*); or two plants (or a plant and an animal) may be mutually helpful, each contributing something of advantage to the other (*mutualism*); or one plant may live at the expense of another plant, or of an animal, deriving nourishment from it, but contributing little or nothing in return (*parasitism*). These various phases or types of symbiosis are indicated in the following table:[1]

Symbiosis
1. Social
   a. Non-nutritive
   b. Nutritive
2. Epiphytism
3. Mutualism
4. Parasitism
   a. Facultative
   b. Obligate

Non-nutritive Social Symbiosis.—A study of vegetation reveals the fact that plants commonly grow in communities, composed of the same or of different species. These communities may result because of (*a*) the habit of growth of the plant, as when the bracken fern (*Pteris*), by the extensive development of its underground rhizomes, comes to occupy a considerable area, sometimes to the complete or almost complete exclusion of other species; or (*b*) because the soil or climate, or both, favor one species or one type of vegetation to the exclusion of others. Thus certain plants, such as *Azalea* or Laurel (*Kalmia*) will grow in communities determined by the acid character of the soil; other plant communities (*e.g.*, of Hawthorn, *Scabiosa*, Milkwort, Red Fescue, etc.) are favored by lime as on the Chalk-downs of England; still others, *e.g.*, Saltwort (*Salsola*), Glasswort (*Salicornia*), Sea Lavender (*Statice*), are favored by salt in the soil, forming "salt-marsh" vegetation. When plants grow together because

[1] The types of symbiosis have been variously classified by different writers.

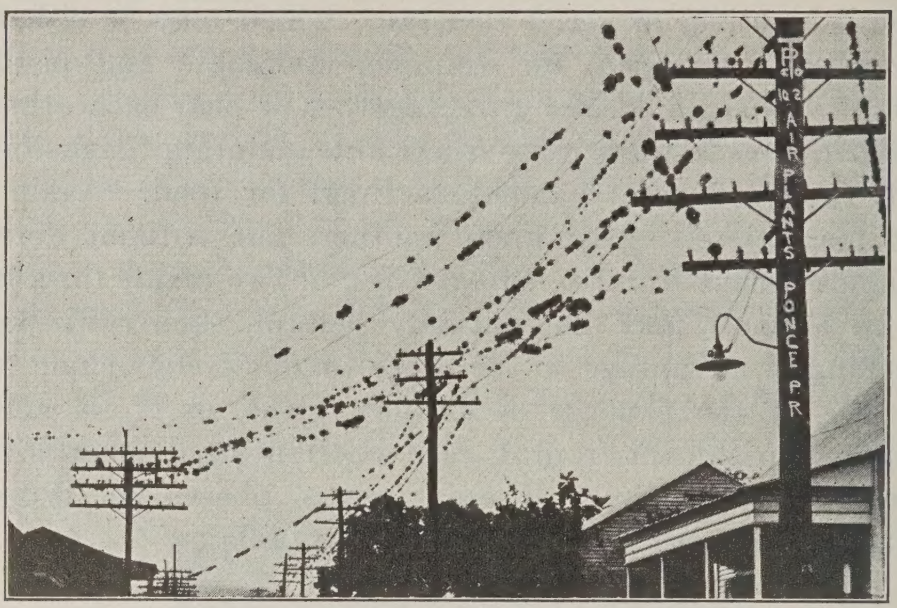


FIG. 119.—Epiphytes or "air" plants (*Tillandsia* sp.), growing on telephone wires at Ponce, P. R.

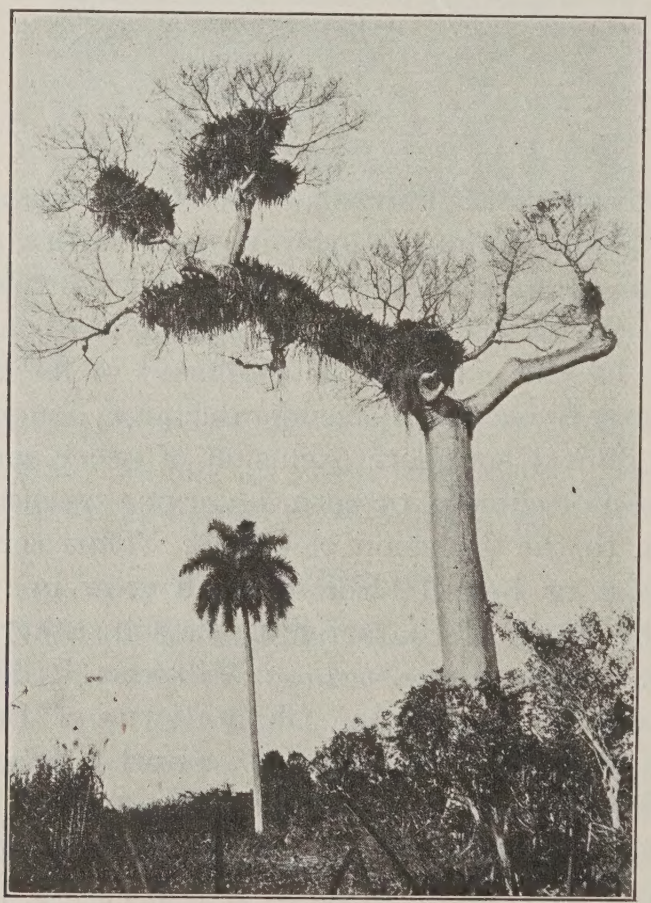


FIG. 120.—Epiphytic group of bromeliads and orchids on a tree, in Cuba. (Photo by M. T. Cook.)

they are similarly favored by the nutritive character of the soil they are called *commensals* (table companions), and the phenomenon is *commensalism;* but the plants do not have any nutritive dependence on each other. A given combination of uniform climatic and soil conditions will favor the development of a plant community of different species having the same growth-form, and known as a *formation.* Of this there are various types, as, for example, bog-formation, the forest, the heath, and others. A formation composed of one species is a *plant association.* Any given crop, as, for example, a cotton field, or corn field, or potato field is a cultivated association.[1]

Nutritive Social Symbiosis.—As an illustration of social symbiosis of a nutritive character may be mentioned the interesting relation established between certain leaf-cutting ants and a filamentous fungus. The ants remove the foliage-leaves from certain trees and use them as "fungus-farms" or "fungus-gardens" —a suitable substratum on which to cultivate a certain fungus, portions of which serve as food for the ants (Fig. 118). The spores are sown by the ants and the "crop" is harvested in a very systematic manner. The loss of leaves, however, is very deleterious to the life of the tree, and certain species (*e.g.*, *Cecropia* and *Acacia*), secrete a substance which is greatly liked by another kind of ants, a smaller, war-like species. These ants, attracted by the much-prized food, make their home on the tree or in special cavities in it, and repel all attempts of the leaf-cutting species to reach the foliage. Such trees are called ant-loving (*myrmecophylous*), or *myrmecophytes.*

One of the most striking cases of this sort is the Bull's-horn Thorn (*Acacia sphaerocephala*) first described in 1873 by Thomas Belt.[2] The stipules are large thorns, resembling, in miniature, the two horns of cattle, whence the common name. A species of ant lives in the hollow thorns and feeds on nectar secreted by glands situated on the leaf-stalk, and also on curious food-bodies born at the tip of each leaflet of the twice-pinnate leaves. Deriving nourishment from the acacia, these ants, in turn, fiercely

[1] The definitions of the terms "formation" and "association," as given above, follow Warming (*Oecology of Plants*, Oxford, 1909).

[2] Belt, Thomas. The Naturalist in Nicaragua. Everymans Library Ed., p. 17.

attack the leaf-cutting ants, and thus protect the plant from injury.

Certain green algae live symbiotically in the tissues of various lower forms of aquatic animals; certain yeasts live normally in the digestive tracts of plant-lice (Aphids), Cicada, and other insects, possibly aiding digestion; while still other species of yeast and bacteria live *within the cells* of other organisms.

FIG. 121.—An epiphytic Clusia. (From photo by G. V. Nash, taken in Haiti).

The case of the *ambrosia beetles* is another interesting illustration of nutritive social symbiosis. There are several species of these beetles belonging to different genera. They have compact cylindrical bodies and excavate small branching burrows or galleries of considerable extent in the wood of various trees. The entrances to these burrows are often called "shot-holes." The galleries of some species open out into thin leaf-shaped chambers. As the burrows are excavated the tiny chips or chankings are passed through the bodies of the borers, but

they do not serve as food. The food is a species of fungus which is known by its common name, *ambrosia*. This fungus is cultivated by the beetles for food, each species of beetle cultivating a different species of fungus.

It is considered that these fungi have been cultivated by the beetles for many ages, until the plant and the insect are each dependent upon the other for their existence. If the fungus is neglected and not regularly eaten by the insect it quickly deteriorates and dies. Both the larvae and the adult insects

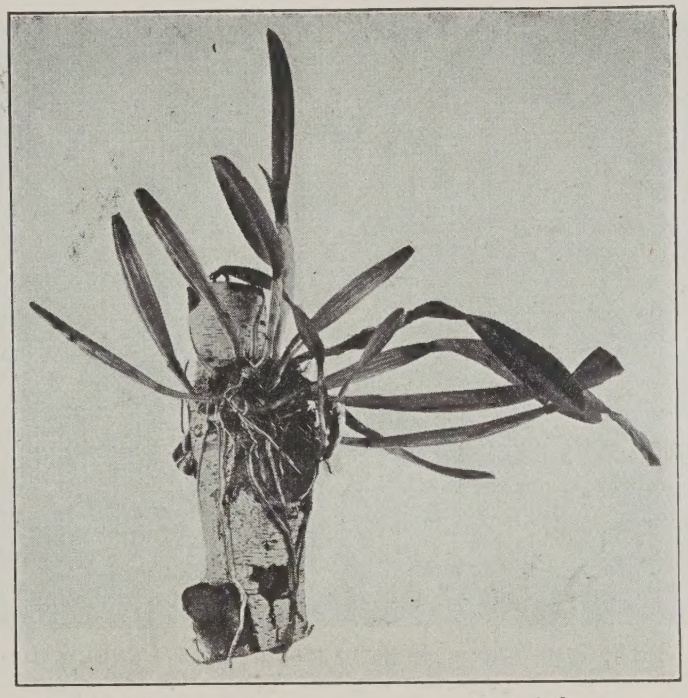


FIG. 122.—An orchid (*Cattleya* sp.) growing as an epiphyte on a portion of a branch of white birch. Note the aerial roots.

feed on the fungus which ceases to be good food if allowed to form spores. The insects carefully prepare a "seed bed" of tiny chips and excrement for sowing the fungus, and if their burrows are disturbed they endeavor to conserve as much as possible of the fungus by eating it, as bees eat their honey when disturbed.

Considerable damage is often done to trees and timber by the ambrosia beetles, but they usually attack only trees or twigs that are dead or dying.

Flowers and Insects.—The dependence of certain plants upon insects to secure cross-pollination is a case of nutritive social

symbiosis, since the insects visit the flowers primarily for the purpose of securing nectar. This matter is treated of in Chapter XVII.

Epiphytism.—Any plant (whether parasite or not) that lives on another, or upon any other convenient support (Fig. 119), is an *epiphyte*, but the term is commonly restricted to those cases where there is no physiological or nutritional relationship between the two. A vine climbing up a tree is an epiphyte, as are also the *Pleurococcus* and mosses growing on the tree trunks. Epi-

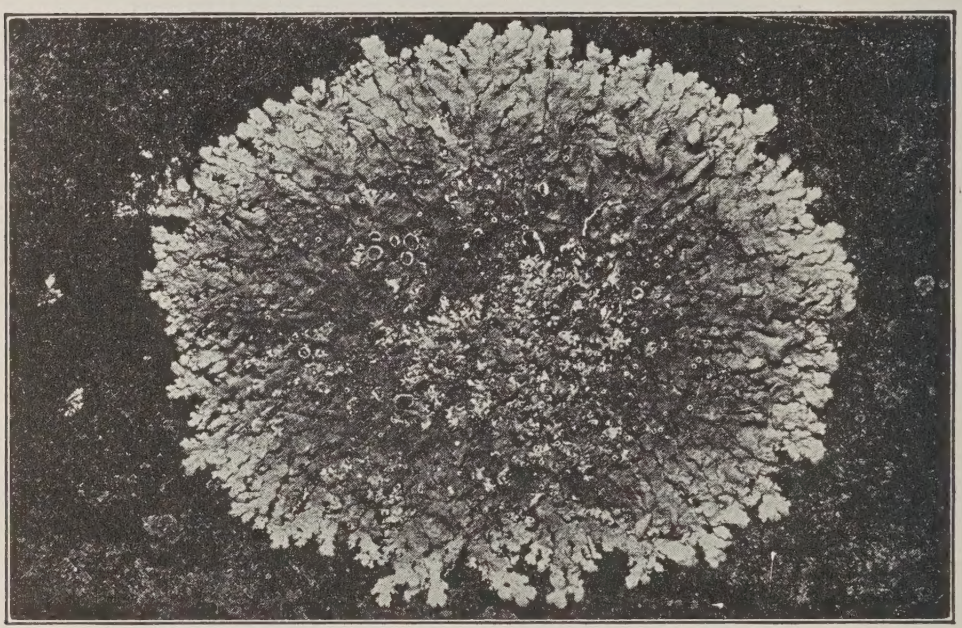


FIG. 123.—A thallose lichen, *Physcia stellaris* (L.) Nyb., growing on a rock. The cup-shaped structures are the fruiting bodies (apothecia). At the left are seen two very young plants.

phytism is specially common in the tropics where orchids, ferns, Hohenbergias, and great *lianas* (vines) are found growing in profusion on other plants (Figs. 120, 121, and 122).

Mutualism.—The associating together of two plants in intimate physiological relationship, to their mutual advantage, is admirably illustrated by *lichens*. These plants grow commonly on the trunks and stems of trees, on old boards and fences, and on rocks (Fig. 123). The plant body is a thallus, and, when its inner structure is examined, it is seen to be a composite plant, formed by a species of alga, resembling *Pleurococcus*, and surrounded by the mycelium of a filamentous fungus (Fig. 124). In a few of the genera the fungal element is a Basidiomycete,

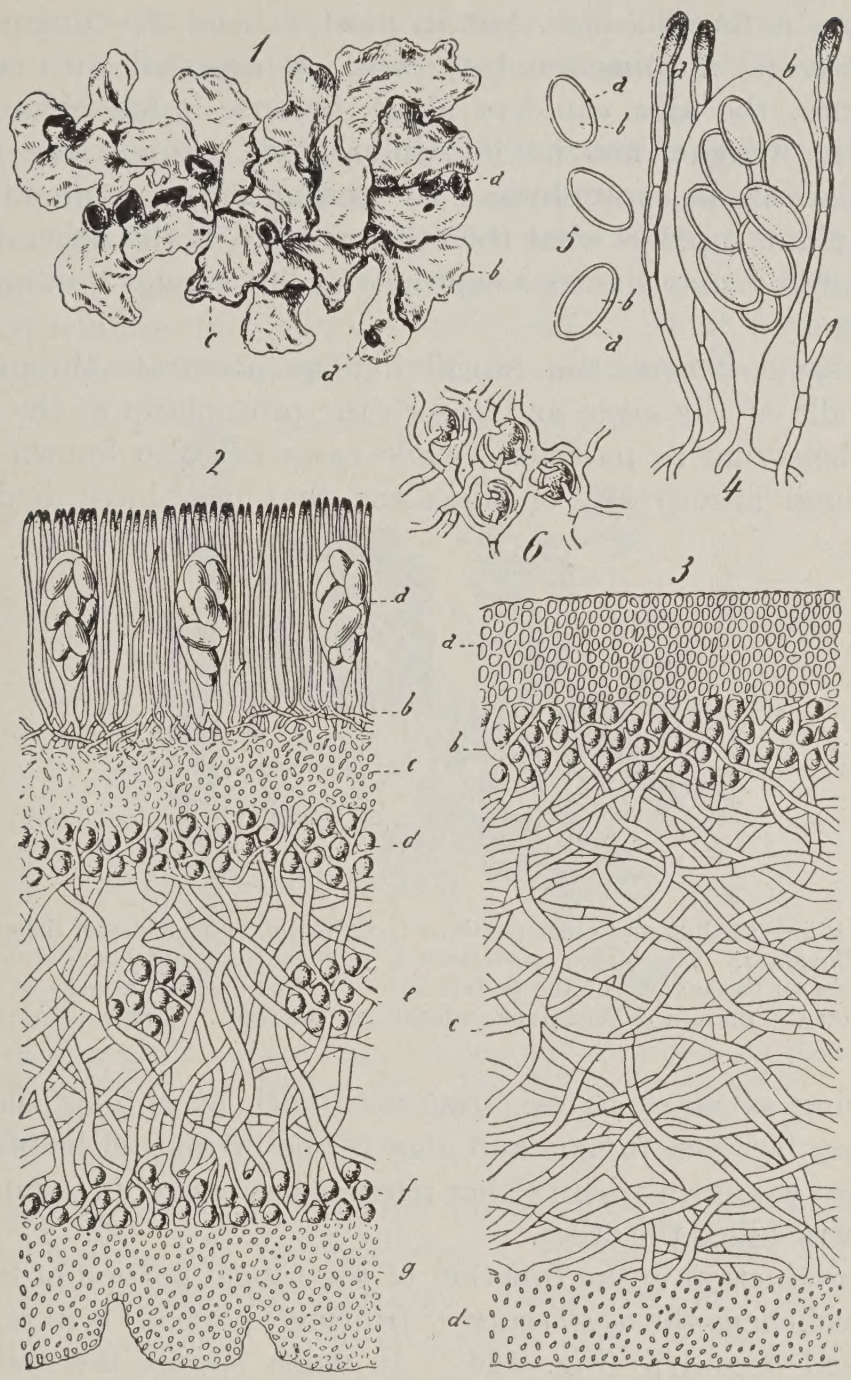


FIG. 124.—A lichen, *Parmelia perlata* (L.) Ach. 1. Plant, slightly reduced in size; *a*, apothecia; *b*, lobe of thallus; *c*, soredial patches. The soredia are vegetative reproductive bodies composed of both algal and fungal elements, and therefore able to reproduce the lichen; the ascospores, alone, cannot do this. 2. Longitudinal section of apothecium; *a*, thecium; *b* and *c*, the two layers of the hypothecium; *d*, upper algal layer; *e*, colonies of algae distributed through the medullary layer; *f*, lower algal layer; *g*, lower cortical layer. 3. Cross-section of vegetative portion of thallus. 4. Paraphyses (sterile fungal filaments), and spore-sac (ascus), containing ascospores. 5. Ascospores. 6, Algal cells, surrounded by fungal hyphae with haustoria (absorbing branches.) (After Schneider.)

forming a *Basidiolichen*, but in most lichens the fungus is an Ascomycete, forming an *Ascolichen*. If supplied with suitable moisture, the alga can live alone, because it has chlorophyll, but the fungus, not having chlorophyll, cannot live except as a parasite or saprophyte. By uniting into a common body, each plant supplies what the other needs. If the lichen-fungus is isolated it may live as a saprophyte, but cannot fruit and produce spores.

In some lichens the fungal hyphae penetrate through the cell-walls of the algae and absorb the protoplasm of the latter, thus behaving as parasites; while cases are also known where the fungi absorb any of the algae that may have died, thus

FIG. 125.—Thallus and erect portions (*podetia*) of two species of lichen of the genus *Cladonia*. The largest podetium is *proliferating*, and bears a number of apothecia on the margin of the podetium of the first rank. Apothecia are also shown on the margin of the larger podetium at the right. (Drawn from nature.)

behaving as saprophytes. But with such exceptions the relationship between fungus and alga is one of mutual helpfulness. No case is known where either partner has entirely consumed or otherwise killed the other.

Reproduction is the function of the fungal portion of lichens. In Ascolichens the *apothecium* ("fruiting" portion) is in reality a modified ascocarp (Fig. 124). In some species the apothecia occur at the summit of specialized, upright branches or *podetia* (Fig. 125).

Only a few years ago the interesting discovery was made that lichens may be experimentally produced by the artificial union of certain algae and fungi (Fig. 126). Some of the lichens thus produced resembled those found in nature, while other combinations were entirely new.

The relation between orchid seeds and the fungus that has been thought to be essential to their germination (p. 921) is also a case of mutualism.

An interesting case of the symbiotic association of four genera, if not to their mutual benefit, at least without apparent detriment to any, is found in the roots of some of the Cycads. All the genera of the Cycad family (*Cycadaceae*) produce branched, coralloid nodules on their roots (Fig. 127). These nodules are caused primarily by infection with the nitrogen-fixing organism,

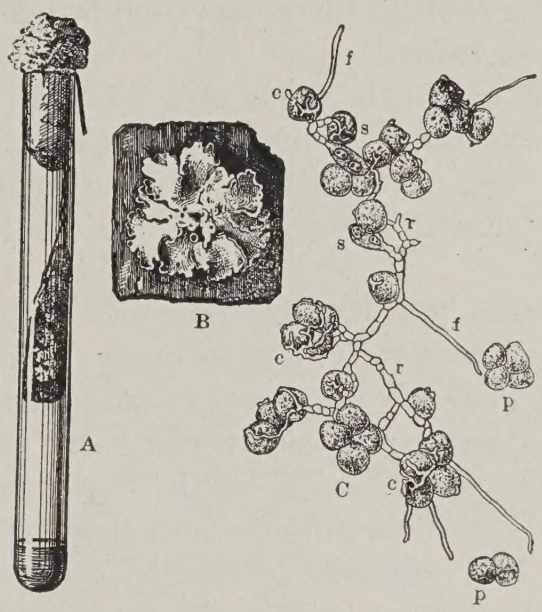


FIG. 126.—A lichen produced synthetically by cultivating the spores of a fungus in association with a green alga. The culture was carried on in a test-tube on sterilized culture media, thus preventing contamination by bacteria and foreign spores. (After Bonnier.)

Pseudomonas radicicola. By the development of lenticels at the base of each nodule the epidermis is ruptured, thus affording entrance to another nitrogen-fixer, *Azotobacter*, and also under favorable conditions, to a blue-green alga (*Nostoc*). This is the only known case in which four organisms are associated together symbiotically. The alga has never been found in the nodules of *Bowenia*, *Ceratozamia*, *Macrozamia*, nor *Zamia*, all genera belonging to the family Cycadaceae.

Economic Importance of Lichens.[1]—Lichens form the main food of numerous wood-lice, mites, and other species of insects; they

[1] Cf. Smith, Annie Lorraine. *Lichens*. Cambridge University Press. England, 1921.

are also commonly eaten by snails, slugs, and other small animals. The well-known "reindeer moss" (*Cladonia rangiferina*), which forms lichen-associations in northern countries, is used rather extensively as food, not only by reindeer, but also by deer, cattle, and other wild animals, and it has been stated that feeding on this lichen has increased the percentage of butter-fat in the milk of certain cows in northern Norway and Sweden. "Iceland moss" (*Cetraria islandica*) is a commercial product from Iceland and Scandinavia, where it is ground to a powder, specially treated to remove a bitter taste, and used to make soups, bread, and other food for man.

In the deserts of North Africa and Western Asia the lichen, *Lecanora esculenta*, called "bread from heaven" is mixed with meal to make bread. This lichen has been thought by some to have been the "manna" which nourished the Israelites during the Exodus.[1]

Lichens have also been used as medicines, as dye stuffs, in the manufacturing of perfumery, and formerly (in colonial times in the United States) as a white powder for the hair.

A case of mutualism between a plant and an animal is that between a fungus and a coccid beetle, the cottony maple-scale insect, *Pulvinaria*.[2] These insects may be found, partly grown, attached to the bark of maples and a few other woody plants in early April. Observation discloses that, at this stage of their development, the fat-bodies of the insect always contain a yeast-like fungus, which has been identified as not a yeast, but as probably a species of *Dematium* or of some related genus. The fungus secretes at least three ferments, namely, diastase, protease, and lipase. It is not positively known in just what way the fungus is of value to the insect, but Brues and Glaser suggest that the

[1] Leo Errera, a noted French botanist, considered that two kinds of manna are referred to in the Bible; the one on which the Israelites fed during the Exodus (*Exodus* XVI) being the sweet gum, produced by species of *Tamarix* (not tamarack); the other (referred to in Numbers XI) being the lichen *Lecanora esculenta*. It has been reported that quantities of this lichen were gathered in 1892 after a heavy hail storm in Mesopotamia.

[2] Brues, Charles T. & Rudolf W. Glaser. A symbiotic fungus occurring in the fat-body of Pulvinaria innumerabilis Roth. Biol. Bull. **40**: 299–318. June, 1921.

diastase may possibly be injected into the tissues of the tree, on which the insect feeds, and thus assist in digesting it; it may also assist in digesting the food after it is taken into the digestive tract of the insect. The fat-digesting enzyme (lipase) must act upon the fat of the fat-body, and may therefore assist in breaking down this body when eggs are being formed at the maturity of

FIG. 127.—Root-nodules of *Cycas revoluta*. *n*, one of several cross-sectional views, showing the zone of the symbiont alga, *Nostoc*.

the insect. The insect is able to inhibit the development of an excess of the fungus, for the number of fungus cells is very uniform and never increases beyond certain bounds. If the fungus were a parasite, this would not, in all probability, be the case. Moreover the fungus is always present in the insect. These, and other considerations, convince the authors cited that we have here a case of true mutualism.

Grafting.—Nutritive symbiosis is artificially brought about by the process of grafting, discussed in Chapter XV. The stock supplies to the cion the necessary water and mineral nutrients from the soil, while the cion supplies to the stock the necessary plant food elaborated by the green leaves. "Natural grafts" are often produced by two branches, of the same or of adjacent trees, rubbing against each other until the bark is worn through and the two cambial layers thus brought into contact.

Mycorrhizas.—The roots of many plants (especially of woody plants) enter into intimate association with the mycelia of various fungi growing in the soil. The mycelia either form a mantle

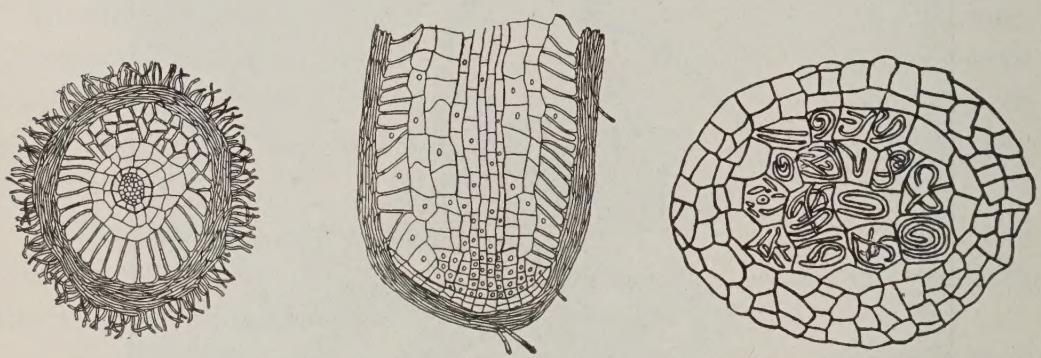


FIG. 128. FIG. 129.

FIG. 128.—Ectotrophic mycorhizas. At left, mycorhizal mantle on root of hickory (*Carya ovata*), in cross-section; at right, root-tip of an oak (*Quercus*), covered by fungus mantle. (After W. B. McDougall.)

FIG. 129.—Tangential section of root of the red maple (*Acer rubrum*), showing endotrophic mycorhiza in the cells. (After W. B. McDougall.)

or jacket at or near the surface of the young roots (*ectotrophic*, Fig. 128), or they penetrate through the cell-walls into the cell-cavities (*endotrophic*, Fig. 129). Recent careful studies seem to demonstrate that the ectotrophic mycorrhizas, common on the roots of many kinds of trees (hickory, oaks, birch, sugar-maple, larch, beech, hornbeam), are, in reality, evidence of the parasitism of some fungus on the tree. Several species of fleshy fungi are, in this way, parasitic or partly parasitic. In ectotrophic infection the hyphae penetrate through the epidermis and then grow and branch underneath it, some of the branches growing between the individual epidermal cells by dissolving the middle lamella with enzymes which they secrete. In this manner there is formed a pseudo-tissue, closely analogous to a lichen, which replaces the true epidermis. The fungus doubtless derives some nourish-

ment from the dissolved (digested) substance of the middle lamella, as well as from nutrient substances that diffuse out from adjacent cells; but there is no evidence that the tree is in any way benefited by the presence of the fungus.

In some cases the development of the mycorrhiza-mantle inhibits the growth of the root, and stimulates a profuse branching, which is repeated as the branches are infected. This gives

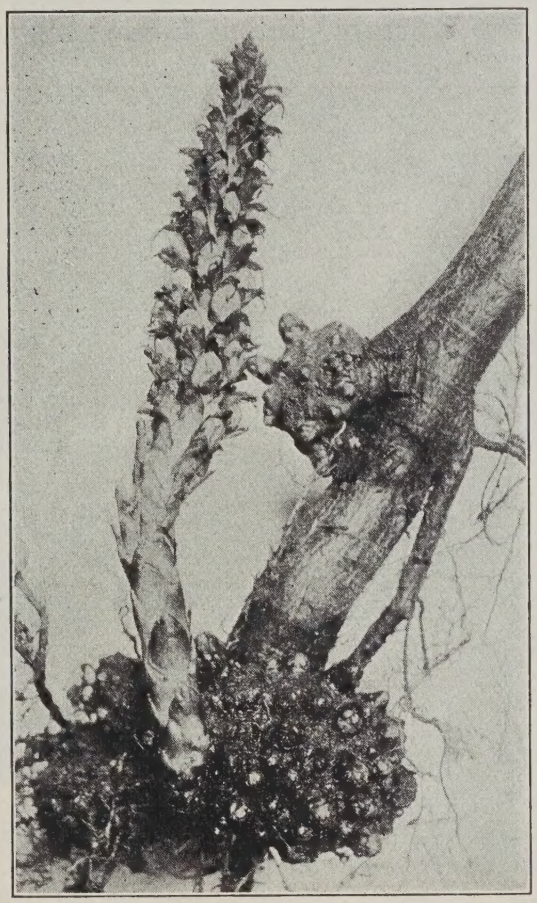


FIG. 130.—Cancer-root (*Conopholis americana*), of the Broom-rape family (Orobanchaceae), parasitic on the root of a flowering plant. The ovaries are developing into capsules. The plant derives its name from the scaly cone. (Photo by Elsie M. Kittredge.)

rise to a malformation known as "coral root," which is so well developed in one herbaceous species as to give the plant its scientific as well as its common name—*Corallorhiza*, or coral-root.

In endotrophic mycorrhizas the hyphae penetrate through the cell-walls into the cell-cavities, and in such cases all stages are found from true parasitism of the fungus on the root, through a mutually beneficial relationship, to a parasitism of the root-cells

on the fungus. Among common trees having endotrophic mycorrhizas, may be mentioned the black maple, horse-chestnut, and black walnut, and most of the heath family (Ericaceae), such as trailing arbutus, huckleberry, wintergreen, heather, laurel, and rhododendron. This is probably the chief reason why it is so difficult to transplant many of the heaths; the delicate adjustment between the plant and the mycorrhizal fungus is disturbed in transplanting, and the soil conditions in the new habitat are not favorable to its reestablishment before the plant dies. The

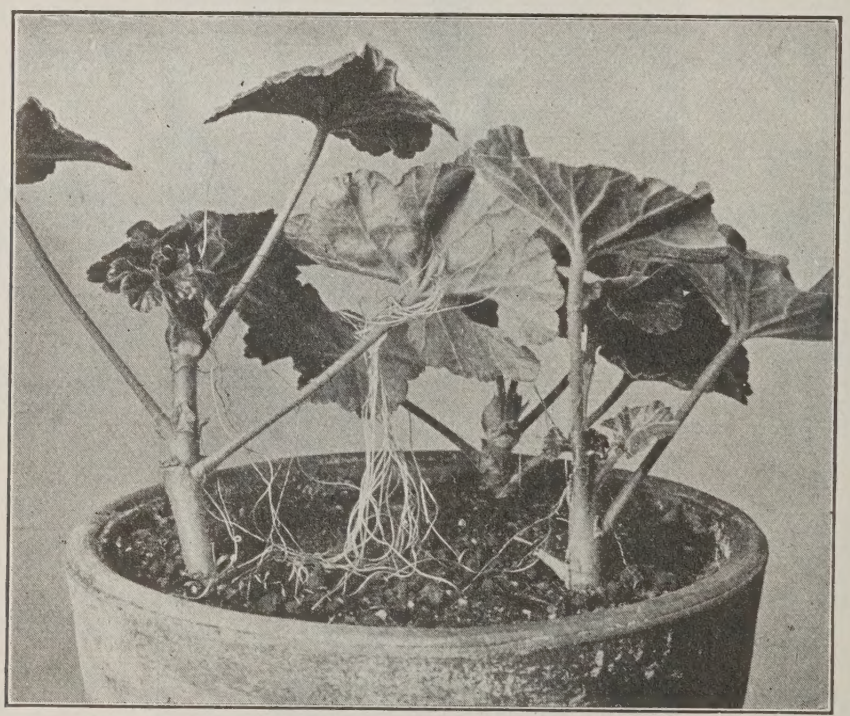


FIG. 131.—Dodder (*Cuscuta* sp.), parasitic on geranium (*Pelargonium*). A few seedlings at the left are still rooted in the soil, and are not yet attached to the host-plant. They eventually sever all relation with the soil.

Indian-pipe and the False Beech-Drops (Figs. 116 and 117), both belonging to the heath family, also possess endotrophic mycorrhizas. They have recently been reported[1] as occurring in the Spruce (*Picea canadensis*), Larch (*Larix laricina*), and other conifers.

Parasitism.—In some cases of symbiosis, as stated above, only one plant derives any benefit from the union, which may or may not be of positive injury to the other. Such is the case with the ectotrophic mycorrhizas, already mentioned. A plant that thus

[1] Lewis, Francis J., in Nature **114**: 860. Dec. 13, 1924.

derives its nourishment from the tissues of another living plant is a *parasite;*[1] the plant lived upon by a parasite is the *host-plant.* There are many instances of the parasitism of one flowering plant on another (Fig. 130). In some of these cases as, for example, the dodder (*Cuscuta*), the parasite may have completely lost the power of elaborating chlorophyll, and thus lack the function of

FIG. 132.—Dodder (*Cuscuta* sp.), in flower. Parasitic on a golden rod (*Solidago ulmifolia*). (Photo by Elsie M. Kittredge.)

photosynthesis; the parasitism is then complete (Figs. 131, 132 and 133). In other cases the parasite may retain its chlorophyll-apparatus, and hence be only partly dependent upon the host, as in the case of the mistletoe (Fig. 134). Such plants are

[1] From the Greek *parasitos* (παράσιτος), one who eats at another's table. From *para* (παρά), beside + *sitos* (σῖτος), wheat, food, bread. The term was first used in botany in 1723 by the Italian botanist, Micheli (1679–1737), in a work on the broom-rape (*Orobanche*). PIETRO ANTONIO MICHELI was director of the botanic garden in Florence, where he was born and died.

hemiparasites. Another example of hemi-parasitism is that of the blue-green alga, *Nostoc*, species of which grow in little pockets or cavities in the tissues of the water-fern *Salvinia*, of *Gunnera manicata*, of the liverwort, *Anthoceros*, and of other plants, without apparent injury to the host (Fig. 127). The parasitism of fungi is amply illustrated in Chapters XXII and XXIII.

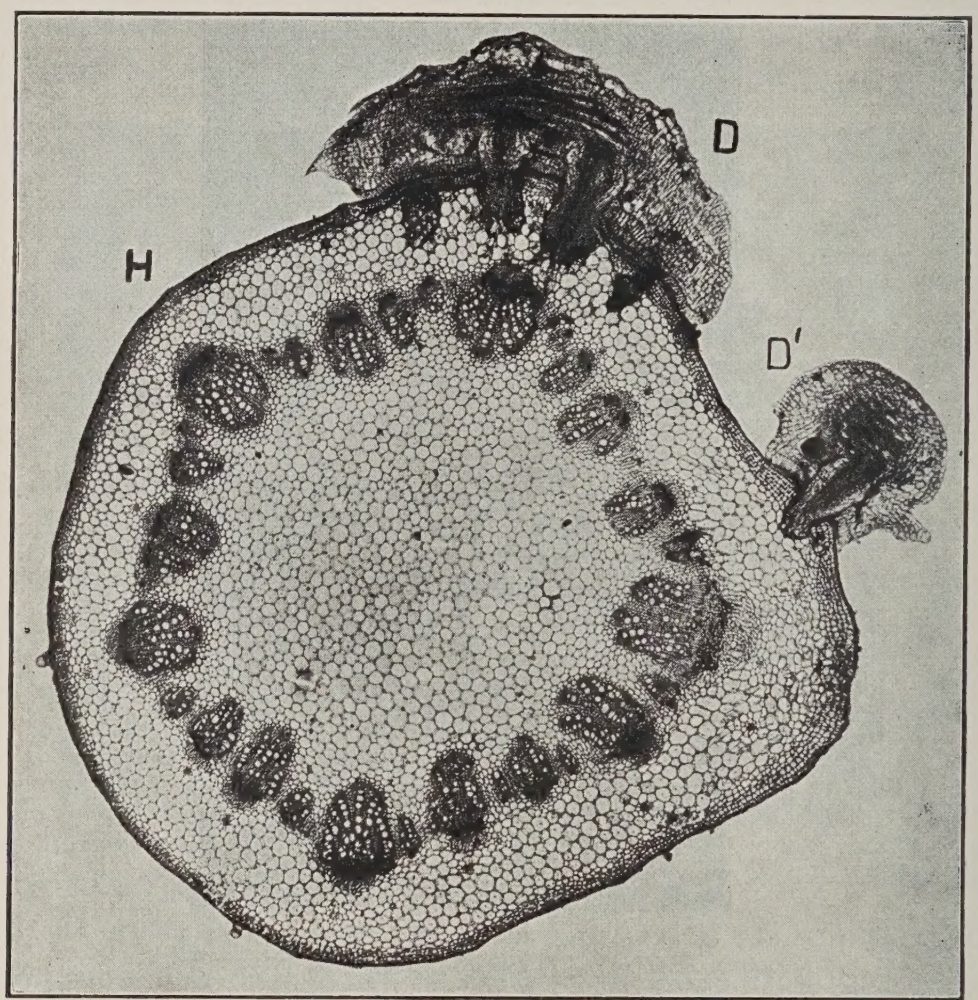


Fig. 133.—Photomicrograph of a cross-section of the stem of a dicotyledonous host-plant infested with the parasite, dodder (*Cuscuta* sp.). Note the haustoria extending from the dodder (D, D′) into the cortex of the host (H). Greatly enlarged.

Animals Parasitic on Plants.—Various species of the unicellular animal, *Herpetomonas*, a flagellate protozoan, live parasitically in the tissues of milkweeds (species of *Asclepias*). How they are transferred from one plant to another is not known. Possibly it is by insects. Widespread injury is done to trees and shrubs by *borers*, the larval stage of various species of insects, living in

cavities which they themselves make in the woody tissues of stems and roots. Not only do the cavities weaken the plant, but their moist surfaces are favorable places for the germination of the spores of fungi, which grow through the tissues of the plant, causing decay.

Another insect, the *leaf-miner*, lives on the mesophyll of foliage leaves. A serious pest to certain bulbous plants is the larva of

FIG. 134.—Cross-section of a branch of live oak, showing five stems of mistletoe, parasitic on the oak; the upper stem with foliage and fruit. Note the prominent "sinkers" of the parasite, some of them growing laterally for a short distance, close under the surface of the bark, and then radially, deep into the tissue of the wood.

the Narcissus-fly, which lives in the bulbs of Narcissus and onions. The larvae in apples and nuts, and the European corn-borer, are well-known and economically important instances of innumerable other examples that might be cited.

Plants Parasitic on Animals.—The parasitism of pathogenic bacteria (which are plants) on animals is, of course, well known.

A common disease of fishes is caused by fungi (species of the water-mold, *Saprolegnia*) growing on the gills and other parts of the fish. Other cases could be cited.

Fungal Parasites.—The entire group of the Fungi, including the smuts, rusts, and other disease-producing fungi, are parasitic on flowering plants. The "shelf-fungi," commonly found on forest trees are economically important because of the enormous financial losses occasioned by the timber-decay which they induce. Fungi and fungal diseases are discussed in Chapters XXII–XXIV.

FIG. 135.—*Cissus laciniata*, parasitic on the cactus (*Opuntia Blakeana*). The parasitism was artificially induced (xeno-parasitism). The host plant has been sectioned to expose the roots of the xeno-parasite. (Redrawn from D. T. MacDougal.)

Artificial Parasites.—By recent experiments certain plants have been induced, by experimental treatment, to grow as parasites on other plants (Fig. 135). The condition necessary to success in such experiments is that the osmotic strength of the cell-sap of the host must be less than, or at least not greater than that of the parasite.

Parasitism Means Degeneration.—Most parasites among the flowering plants have suffered the loss of some organ or organs, and of one or more functions, in connection with acquiring the parasitic habit. In fact, parasitism must be regarded as an

acquired habit, and the parasite among plants, as in human society or elsewhere, as a degenerate form of life. The following lists illustrate the two kinds of parasitism, as indicated:

Facultative Parasites	Obligate Parasites
Blue-green algae (*Nostoc sp.*)	Dodder (*Cuscuta*)
Damping-off-fungus (*Pythium*)	American Mistletoe (*Phoradendron villosum*)
Some timber-destroying fungi (*e.g.*, *Armillaria mellea*)	Broom-rape (*Orobanche*)
Some molds (*Mucor sp.*, and *Penicillium sp.*)	European Mistletoe (*Viscum album*)
Late blight of Potatoes (*Phytophthora infestans*)	Root-tubercle organisms
	Rusts (*Uredineae*)
	Smuts (*Ustilagineae*)
	Ergot of grain.

CHAPTER XII

THE NITROGEN PROBLEM

The Importance of Nitrogen.—No plant can mature without nitrogen; it enters into the composition of the protein foods required by plants, and is an essential component of protoplasm, chlorophyll, gluten, and other plant substances. No plant cell can live without it. Since it is necessary to chlorophyll formation, a deficiency of nitrogen is accompanied by a yellowing of the foliage and a decrease or cessation of photosynthesis; thus the elaboration of carbohydrates is dependent on a suitable supply of nitrogen. It is also an invariable component of the decayed animal and vegetable matter of the soil, known as *humus*, an essential factor in soil fertility. Furthermore, nitrogen is the most expensive essential element to replenish as the supply falls off.

The Need of Nitrogen.—The amount of nitrogen required by plants is illustrated by the data in the following table, showing

TABLE VI.[1]—PLANT FOOD IN WHEAT, CORN, OATS, AND CLOVER

Crop		Nitrogen, lbs.	Phosphorus, lbs.	Potassium, lbs.	Magnesium, lbs.	Calcium, lbs.
Kind	Amt.					
Wheat grain	50 bu.	71	12	13	4	1
Wheat straw	2½ tons	25	4	45	4	10
Corn grain	100 bu.	100	17	19	7	1
Corn stover	3 tons	48	6	52	10	21
Corn cobs	½ ton	2	..	2		
Oats grain	100 bu.	66	11	16	4	2
Oats straw	2½ tons	31	5	52	7	15
Clover seed	4 bu.	7	2	3	1	1
Clover hay	4 tons	160	20	120	31	117

[1] Hopkins, Cyril G., *et al.* Univ. Illinois. Agr. Exp. Sta. Soil report, No. 18. Nov. 1918.

the results of analyzing various kinds of plant tissue. Figures are given, not only for nitrogen, but also for the four metallic elements with which it is commonly found united or associated in plant tissue.

Analyses by Hopkins also show that the following amounts of nitrogen are required for the produce named:

1 bushel of oats (grain and straw) requires of *nitrogen*	1	pound
1 bushel corn (grain and stalks) requires of *nitrogen*	1½	pounds
1 bushel wheat (grain and straw)requires of *nitrogen*	2	pounds
1 ton timothy requires of *nitrogen*	24	pounds
1 ton clover requires of *nitrogen*	40	pounds
1 ton cowpeas requires of *nitrogen*	43	pounds
(1 ton of average manure contains	10	pounds)

The tops (shoots) of clover contain about twice as much as the roots, while the tops of cowpeas and soybeans contain about 74% as much as the roots, *at the time of harvest.* In younger plants the tops contain much less than the roots.

Loss of Nitrogen by Cropping.—Whenever a given crop is harvested the chemical elements which it has obtained from the soil are, of course, thereby removed in whole or in part, and the soil correspondingly impoverished. The loss of nitrogen from this cause may readily be inferred from the figures just given. Examples might be multiplied. Thus, the average yield of wheat in the United States is about 14 bushels per acre.[1] Such a crop will remove (in the grain and straw) between 28 and 30 lbs. of nitrogen, nearly 14 lbs. of potash, and over 9 lbs. of phosphoric acid. If all these elements were in available form, soil analyses show that the first 8 inches of average soil contain enough potash to last 1000 years, enough phosphoric acid for

[1] An increase of a little over 2 bu. over the average of 11.9 bu. for the decade from 1866–1875. The average yield in bushels per acre in certain foreign countries was as follows: 1886–1895, Holland, 27.70; Denmark, 37.30; 1896–1905, Holland, 31.20; Denmark, 40.60; 1898–1907, France, 20.8; United Kingdom, 32.60. In 1910 the yield per acre was 29.70 bu. in Maine, 29.30 in Vermont, 23.70 in New York, and 25.0 in Wyoming. How far the average of 14.0 bushels per acre falls below possible yield is evident by comparison with the yields of 48.0 bu. and 48.50 bu. obtained in 1905 on two experimental plots in the corn belt region of the Illinois prairie. (*Hopkins.*)

500 years, but only enough combined nitrogen for 90 years. The maintenance of the nitrogen supply, therefore, is a most pressing problem, and extensive investigations have been carried out under the direction of our own and foreign governments with a view to ascertaining an efficient method of recovering, for agricultural and commercial use, the vast store of nitrogen in the earth's atmosphere. While much of the nitrogen is removed when crops are harvested, the soil is still further impoverished by the removal of nitrogen compounds, by drainage, the decay of humus, the removal of surface soil by wind,[1] and in other ways. Snyder, at the Minnesota Agricultural Experiment Station, demonstrated that, during a period of 15 years, certain Minnesota soils lost, in these and other ways, from three to four times as much nitrogen as was removed by the crops.[2] Thus it was estimated that, on certain experimental plots, an acre of soil to a depth of nine inches contained approximately 7700 lbs. of nitrogen. During 15 years of continuous wheat crops, the total loss of nitrogen was 3000–5000 lbs. of which only 750 pounds were removed in the crop, leaving 2250–4250 lbs. which were lost through other causes mentioned above, and in this case chiefly through the decay of humus by which the nitrogen was transformed into gaseous and easily soluble forms, removed from the soil by diffusion and leaching. The gradual decline of fertility of the rich virgin prairie soils of the United States is doubtless due chiefly to this cause, brought about by the continuous cultivation of crop after crop of wheat, corn, and other cereals. On a field at Rothamsted a small plot of arable land kept free from crops and weeds for 35 years by hoeing was found to have lost one third of its original nitrogen. The total loss of nitrogen, in pounds, was 1050, of which 940 lbs. were lost as nitrates by leaching. In

[1] The quantity of soil transported by wind is far greater than might ordinarily be supposed. Thus, for example, evidence has recently been adduced by Harrison (West Indian Bull. **18**: 77–98. 1920) indicating that the high-level soil of Barbados (West Indies) owes its origin directly or indirectly to the air-borne debris of the volcanoes of St. Vincent and other vents of the West Indian volcanic province. During four eruptions from 1812–1903, as much as 2.78 lbs. of volcanic ash were added to each square foot of soil. The low-level soils are considered to have had a similar origin.

[2] Snyder, H. Univ. of Minn. Agr. Exp. Sta. Bulls. 30 (1893), 41 (1895), 53 (1897), 65 (1899), 70 (1901).

other words, the largest loss of nitrates is due to leaching; the second largest loss is due to crop removal.

Sources of Nitrogen.—Among the various sources of nitrogen important for agriculture there may be mentioned the following:

1. Manure and other fertilizers.
2. Organic nitrogenous compounds in the soil.
3. The free nitrogen of the air.

1. Some of the nitrogen is returned to the soil when manure is used, but large quantities are purchased in the form of commercial fertilizers, containing potassium nitrate (saltpeter), calcium nitrate, ammonium sulphate (containing about 20% of nitrogen), sodium nitrate (containing about 15%), and other ingredients. The purchase of nitrogen, however, is an expensive method, for in the form of commercial fertilizers it costs over 20 cents a pound—an amount sufficient to produce less than one bushel of corn. Moreover, much of the nitrogen in this form is imported from abroad into the United States. About fourteen years ago (1910) the importations of sodium nitrate alone, the most important of the salts mentioned above, amounted to 16½ million dollars.[1] Now, it has been stated[1] that the total world's supply of this compound is less than 450 billion pounds, but it has been calculated that, for the one year 1910, the following nine crops—corn, wheat, oats, barley, rye, potatoes, hay, cotton, and tobacco—required 11½ billion pounds of nitrogen, an amount sufficient to exhaust the world's supply in about forty years. Obviously, a method which steadily exhausts the total supply and at steadily mounting cost, is not rational for practical, permanent agriculture.[2]

[1] This was for importations from Chile alone. Norton, Thomas H. Dept. of Commerce and Labor. Bur. of Manufactures. Special Agent Series, No. 52, p. 9. Washington, 1912. See also

Chile's wealth in nitrate deposits. Review of Reviews, **41**: 485-486. April, 1910. Sodium nitrate ($NaNO_3$) is often called "Chile saltpeter" to distinguish it from saltpeter or niter, which is potassium nitrate (KNO_3).

[2] Small quantities of ammonia and nitrate are continually being formed in the air by the combination of atmospheric nitrogen with hydrogen and oxygen. By an analysis of 81 samples of rain and 29 samples of snow, representing a total annual precipitation of 35.59 inches, Shutt found that a little over 5.84 lbs. of nitrogen per acre were thereby supplied. (*Canada Exp. Farms Report*, p. 51, 1919.)

2. We turn, therefore, to the second of the three sources mentioned above—the organic nitrogenous compounds in the soil. These exist in the form of undecayed plant and animal parts —roots, leaves, stems, animal tissue, and humus which results from the decay of these. But at once we note that these substances are all insoluble, and are hence not available to plants. They must, therefore, be disintegrated and the nitrogen transformed into simpler and soluble compounds. This process, commonly spoken of as decay, is accomplished by the action of bacteria, in a series of three steps, as follows:

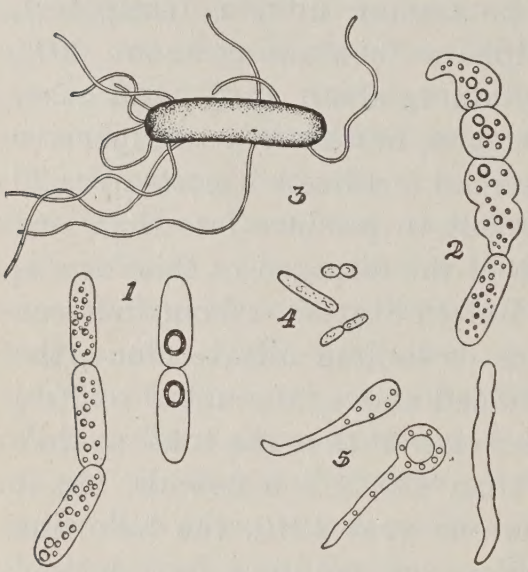


FIG. 136.—Various forms of ammonifying bacteria. (Nos. 1, 2, 4, and 5 after Nadson; No. 3 after Myer. From Lipman.)

a. Production of Ammonia.—The bacteria common on hay (*Bacillus subtilis*), another form common on potatoes (*Bacillus mesentericus vulgatus*), a form very common in soil (*B. mycoides*), and about fifteen or twenty other species (Fig. 136), secrete protein-dissolving (*proteolytic*) enzymes which are able to break up the relatively large protein molecules of the organic compounds in soil, thus producing albuminoses, peptones, urea, and amino-acids, by further change of their molecules, setting free ammonia (NH_3), which may be dissolved in the soil-water, forming ammonium hydroxide ($NH_4(OH)$), such as is commonly sold under the trade name "household ammonia." By the same process considerable carbon dioxide is also produced, and this, dissolved in the soil-water, becomes carbonic acid. When ammonia and carbonic acid are brought together, ammonium carbonate is formed. Experiments of various investigators have proved that numerous fungi also produce ammonia by causing the decomposition of organic matter in the soil. The fungi most active in this are species of *Monilia*, while among the least active are species of *Aspergillus*.

When the soil is deficient in organic remains the lack is supplied by adding suitable quantities of dried blood, tankage,

ground cotton seed, ground fish, bone meal, guano, kelp (a brown seaweed), or other manure.

For the successful production of crops, however, nitrogen must be present in the form of nitrates, such as potassium nitrate (KNO_3), calcium nitrate ($Ca(NO_3)_2$), ammonium nitrate (NH_4NO_3) and others. The formation of nitrates from ammonia (*nitrification*), was at first thought to be a chemical process not involving any vital factor, but in 1862 Pasteur showed that a vital factor was involved. Experimental verification of this was not made until fifteen years later when Schlössing and Müntz showed that, while nitrates are formed when ammonia is passed through soil in long tubes, none is formed if the soil is first sterilized so as to kill all living organisms. Winogradsky, a Russian, working in the Pasteur Institute, Paris, extended these investigations and showed (1890) that the process is brought about by certain species of bacteria to which he gave the names indicated above. The work of Schlössing and Müntz showed that the process depends upon bacteria, while Winogradsky was the first to obtain a pure culture of the bacteria.

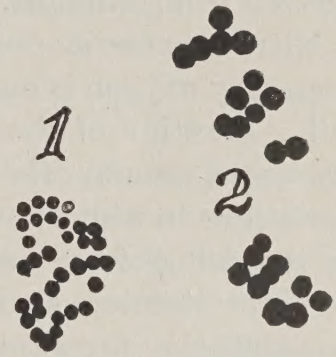


FIG. 137.—Nitrifying bacteria: 1 *Nitrosomonas*, a nitrite bacterium, which changes ammonia to a nitrite; 2 *Nitrobacter*, a nitrate bacterium, which changes a nitrite to a nitrate. (After Burri and Stutzer from Lipman.)

b. Formation of Nitrous Acid and Nitrites.—In addition to ammonifying bacteria there are present in the soil other forms which bring about the formation of nitrous acid by oxidizing ammonia or ammonium compounds, as illustrated in the following equations:[1]

(1) Ammonia + Oxygen = Nitrous acid + Water

$$2NH_3 + 3O_2 = 2HNO_2 + 2H_2O$$

(2) Ammonium carbonate + Oxygen = Nitrous acid + Carbonic acid + Water

$$(NH_4)_2CO_3 + 3O_2 = 2HNO_2 + H_2CO_3 + 2H_2O$$

So far as known, these reactions are brought about, in the soils of America and Australia, by an enzyme secreted by one

[1] As in all such cases, the effect is produced, not by the bacterial cells directly, but by the liquid ferments or enzymes which they secrete.

and only one kind of bacterium, which Winogradsky called *Nitrosomonas* (Fig. 137). In the soils of Africa and Eurasia the form is *Nitrosococcus.*

From the standpoint of the bacteria themselves the oxidation of ammonia or of ammonium compounds is the process by which they obtain the energy necessary for the synthesis of organic out of inorganic compounds—for the building up and repair of their own substance. As stated in Chapter X, this process, called *chemosynthesis* (synthesis by chemical energy), is analogous to the process of *photosynthesis* in green plants, where the energy is derived from sunlight.

Nitrite bacteria also require oxygen, and the supply of the necessary oxygen is one of the numerous advantages of tilling the soil. Aeration of the soil is also insured by two other physical processes, namely, the rising and lowering of the water table and variations in atmospheric pressure. Air is forced out of the soil by the rising of the water table and by a decrease in atmospheric pressure; it enters again when the water table lowers or when the atmospheric pressure increases. Temperature changes also contribute to this result, since the soil-air expands and part of it leaves the soil when heated; it contracts when cooled, thus permitting fresh air to enter from without.

Since nitrite bacteria cannot thrive in a strongly acid medium, it is fortunate that the nitrous acid, formed as above, is constantly neutralized by one or more of the alkaline substances or bases, such as calcium, potassium, magnesium, and others commonly found in soils. When nitrous acid is neutralized by a base the result is a nitrite—*e.g.*, calcium nitrite ($Ca(NO_2)_2$), potassium nitrite (KNO_2), and others, depending upon what base is present. This process is favored by adding to the soil lime (calcium carbonate) and potash (potassium carbonate)—the chief constituent of wood ashes; it proceeds according to the following equation:

	Nitrous acid		Potassium carbonate		Potassium nitrite	Carbon dioxide	Water
(3)	$2HNO_2$	+	K_2CO_3	=	$2KNO_2$	+ CO_2 +	H_2O

c. Formation of Nitrates.—The last stage in nitrification is the oxidation of nitrous acid and nitrites to form nitric acid and nitrates, as illustrated by the following equations:

	Nitrous acid		Oxygen		Nitric acid
(4)	$2HNO_2$	+	O_2	=	$2HNO_3$
	Potassium nitrite		Oxygen		Potassium nitrate
(5)	$2KNO_2$	+	O_2	=	$2KNO_3$

The nitric acid becomes neutralized by union with a base such, for example, as potassium or calcium carbonate, forming potassium or calcium nitrate, carbon dioxide, and water, as shown in equations (6) and (7).

	Nitric acid		Potassium carbonate		Potassium nitrate		Carbon dioxide		Water
(6)	$2HNO_3$	+	K_2CO_3	=	$2KNO_3$	+	CO_2	+	H_2O
	Nitric acid		Calcium carbonate		Calcium nitrate				
(7)	$2HNO_3$	+	$CaCO_3$	=	$Ca(NO_3)_2$	+	CO_2	+	H_2O

As brought about in the soil, these are also *biochemical processes*, depending upon the chemosynthesis of nitrate bacteria of the genus *Nitrobacter* (Fig. 137). Were it not for the nitrite bacteria and the changes they accomplish, the nitrate bacteria could not exist, for they are obliged to obtain their energy by oxidizing nitrites, and cannot oxidize either ammonia or ammonium compounds.

All of the nitrifying organisms are aerobic (*i.e.*, require a plentiful supply of free oxygen); they are most plentiful and vigorous in the upper 6 to 8 inches of the soil, and are seldom found below 18 or 20 inches. The importance of keeping the soil well-drained, and in a good state of tilth is, therefore, evident. Experiments of King in 1909, demonstrated that deep plowing (8–10 inches) tends to increase the number of soil bacteria and also their activity—*e.g.*, the rate of production of ammonia. On the other hand, deep plowing tends to decrease denitrification. The number and activity of the bacteria increase with the temperature of the soil.

Summary.—To recapitulate, the steps in the formation of nitrates are as follows:

1. The bacterial disintegration of organic compounds derived from plant and animal tissues, forming, among other substances, *ammonia.*
2. The biochemical oxidation of ammonia forming *nitrous acid.*
3. The neutralizing of nitrous acid forming *nitrites.*

4. The biochemical oxidation of nitrous acid and nitrites, forming nitric acid and *nitrates.*

5. The absorption of nitrates by plant roots, and their transformation within the plant into *nitrogenous organic compounds,* like those with which we started.

Soil Bacteria and Phosphates.—We have noted above that phosphorus is one of the elements necessary for plant life. It is as necessary for the nitrifying bacteria as for crop-plants, and one of the cheapest forms in which it can be supplied to crops is raw rock-phosphate, which consists chiefly of tricalcium phosphate—$Ca_3(PO_4)_2$. This compound, however, is practically insoluble in soil water, and yet it has been proved by careful experiments that phosphorus supplied in this form does become available to plants. Evidently some process must occur in the soil to bring about this result. It was demonstrated by experiments of Hopkins and Whiting[1] that nitrous acid, formed by the oxidation of ammonium compounds by the nitrite bacteria, can transform the insoluble tricalcium phosphate into soluble monocalcium phosphate—$CaH_4(PO_4)_2$, giving rise at the same time to calcium nitrite, as shown in the following equations:

	Ammonium sulphate		Oxygen		Nitrous acid		Sulphuric acid		Water
(8)	$2(NH_4)_2SO_4$	+	$12O$	=	$4HNO_2$	+	$2H_2SO_4$	+	$4H_2O$

	Nitrous acid		Tricalcium phosphate		Monocalcium phosphate		Calcium nitrite
(9)	$4HNO_2$	+	$Ca_3(PO_4)_2$	=	$CaH_4(PO_4)_2$	+	$2Ca(NO_2)_2$

The sulphuric acid (equation 8) also acts on the insoluble tricalcium phosphate to form soluble monocalcium phosphate and calcium sulphate, and the carbon dioxide also produced by bacterial action, becoming carbonic acid when dissolved in soil water, or dissolved from the air and carried into the soil by rain water, also transforms the insoluble calcium phosphate to the soluble. These results are due to the action of nitrite bacteria, but are not caused by the ammonia-producing bacteria nor by the nitrate bacteria.

Crop-plants That Use Ammonia.—Until very recently it has been thought that nitrogen was "available" to plants *only* in

[1] Hopkins, Cyril G. and Albert L. Whiting. Soil bacteria and phosphates. Univ. of Illinois Agr. Exp. Sta. Bull. No. 190. Urbana, Illinois. June, 1916.

the form of nitrates, but it has recently been claimed that various kinds of cultivated plants can produce normal growth when supplied with nitrogen only in the form of ammonium salts, and under conditions which make nitrification (as defined above) impossible. While most plants (*e.g.*, buckwheat) do best when their nitrogen is supplied in the form of nitrates, others, it is stated, appear to thrive equally well when supplied only with ammonium salts. For example, recent experiments seem to indicate that corn (*Zea Mays*) and "paddy" rice prefer ammonium salts to nitrates, though thriving best when both forms of nitrogen were supplied together.[1]

In recent experiments at the University of Illinois Experiment Station no evidence was found to support the view that farm crops in the corn belt soils of Illinois could utilize ammonia, at least to any practical extent.[2]

However, experiments by several Japanese and other investigators, and later by Kelly,[3] have apparently established the fact that rice prefers ammonia nitrogen to nitrate nitrogen. When nitrates (*e.g.*, sodium nitrate) are applied to rice soil they are reduced to nitrites; the latter accumulate in the soil and act as poisons to the rice plants. No satisfactory explanation of this peculiarity of rice has yet been obtained, but it would seem to be a fortunate adaptation that a crop growing normally in a soil under water (or thoroughly saturated) can utilize ammonia, since in such a soil the aerobic nitrite bacteria cannot live, while those producing ammonia by decay find there a favorable anaerobic environment.

Direct Utilization of Free Nitrogen by Green Plants.—The history of the nitrogen problem affords a striking illustration of the need of extreme care in estimating the value of evidence, and also of the fact that one should always hold himself in readiness to revise even ideas long accepted as valid in the light of new *and trustworthy* evidence. About 1850 Boussingault,

[1] Hutchinson, H. B. and N. H. J. Miller. Jour. Agr. Sci. **3**: 192. Oct., 1909.

[2] Whiting, Albert L. and Warren R. Schoonover. Nitrate production in field soils in Illinois. Univ. Illinois Agr. Exp. Sta. Bull. 225. March, 1920.

[3] Kelly, W. P. The assimilation of nitrogen by rice. Hawaii Agr. Exp. Sta. Bull. 24, 1911.

a noted French investigator, taught that green plants do not assimilate the free nitrogen of the air. Another French investigator, Ville, contended that the evidence pointed to the opposite conclusion. The ideas of Boussingault finally prevailed, and the work and name of Ville became practically unknown to plant physiology. Recent careful studies, however, appear to indicate that Ville was right. Mameli and Pollacci in Italy, Moore, Webster, and Lipman in America, and other workers have recently adduced a large amount of evidence, based on careful experimentation, which indicates that the ability of plants to utilize the free nitrogen of the air is more general than has been believed, and is possessed by green algae, lichens, mosses, aquatic ferns, and aquatic and terrestrial flowering plants, including radish (*Raphanus sativus*), cucurbits (*Cucurbita Pepo*), buckwheat (*Fagopyrum esculentum*), box elder (*Acer negundo*), wheat (*Triticum*), and other species.[1]

Denitrification.—Attention has already been called (p. 224) to the loss of nitrates by leaching, but experiments on the Broadbalk field at the Rothamsted Experiment Station (England) showed enormous losses of nitrates, even when there was no evidence of any great amount of leaching.[2] In the breaking up of a field of prairie land in Western Canada, Shutt found that, after 22 years of cultivation, there was a loss of 2190 lbs. of nitrogen per acre, of which only 700 lbs. were removed by the crops, leaving a dead loss of 1490 lbs. or about 68 lbs. a year. In experiments at the Minnesota Experiment Station, with a system of continuous cropping, it was found that the total loss of nitrogen was 171 lbs. per acre, of which only 24.5 lbs. were removed in the crop. These losses are accounted for in part by the process of *denitrification.* This is also a biochemical process. The active organisms include *Bacillus* (*Denitrobacterium*) *denitrificans, Bacterium fluorescens,* and numerous others.

As a result of bacterial action the plant and animal tissues in the soil undergo decay. In this process protein and other complex nitrogenous compounds are reduced to simpler compounds,

[1] Mameli de Calvino, Eva. The direct assimilation of free nitrogen by plants. Torreya **23**: 99–104. Nov.–Dec., 1923. Includes a bibliography of earlier papers.

[2] Russell, Edward J. Soil conditions and plant growth. London, 1917.

and finally to ammonia (NH_3). The ammonia is still further acted on by *denitrifying bacteria*, and separated into its components, hydrogen and nitrogen. The net result of the bacterial actions just described is the transformation of all nitrogenous compounds to free nitrogen gas, which is returned to the atmosphere. Some process is necessary, therefore, by which the free nitrogen may be again withdrawn from the great reservoir of the air, and built up into compounds available for plant nutrition. The importance of such a provision in nature can hardly be overstated. Without it, all nitrogenous compounds would shortly be reduced to ammonia and free nitrogen, for the most part not available to plants, and then, of necessity, all plant life and hence all animal life, would cease. Thus, while so much of the sickness, suffering, and sorrow of the world are due to certain kinds of bacteria (the pathogenic forms), we are quite dependent on other forms for our daily bread, and for the prosperity and happiness that depend upon efficient crop-production.

Nitrogen-fixation.—So far as the needs of plants are concerned, the supply of free nitrogen in the air is inexhaustible. It has been calculated that the air over one acre of ground contains about seventy-five million pounds, or enough to meet the needs of fifty million bushels of corn, or three and three-fourths millions bushels of wheat.[1] At the present rate of requirement, this would meet the world's needs for about 50 years. "Of this enormous reserve," says Norton, "a minute fraction, about 0.000002, is in the active service of the vegetable and animal kingdoms." Since the nitrogen used by plants (and then by animals) passes continuously from the air to plants and thence back to the air again, it has been termed "nomadic nitrogen." As a result of the action of atmospheric electricity about 100,000,000 tons of combined nitrogen (nitric acid) are restored annually to the soil. This amounts to only about 0.3 to 0.4 gram per cubic yard. If only one per cent. of this could be conserved for the use of crops the nitrogen problem would be solved, but such is not the case.

[1] Over each square mile of the earth's surface there are more than 26,600,000 tons of nitrogen, and the total area of the earth's surface is 199,712,000 square miles. *Cf.* p. 225, footnote 1.

Leguminous Tubercles.—For the important work of recovering the free nitrogen of the air (*nitrogen fixation*) in sufficient quantity for plant needs, we are again dependent upon bacteria, and notably upon *Bacillus radicicola* Beijerinck (*Pseudomonas radicicola* (Beijerinck) Moore). At one stage of its existence this organism is found in the form of tiny,[1] motile, rod-shaped bodies in the soil. When the roots of legumes (such as clover, lupine, locust, peas, beans, alfalfa, cowpea, soybean, etc.) are present the bacteria enter through the root-hairs (Fig. 138), and penetrate into the tissues of the root, stimulating the growth of the tissue in such a way as to form nodules,[2] which become filled with the rapidly multiplying organisms. In the nodules the organisms

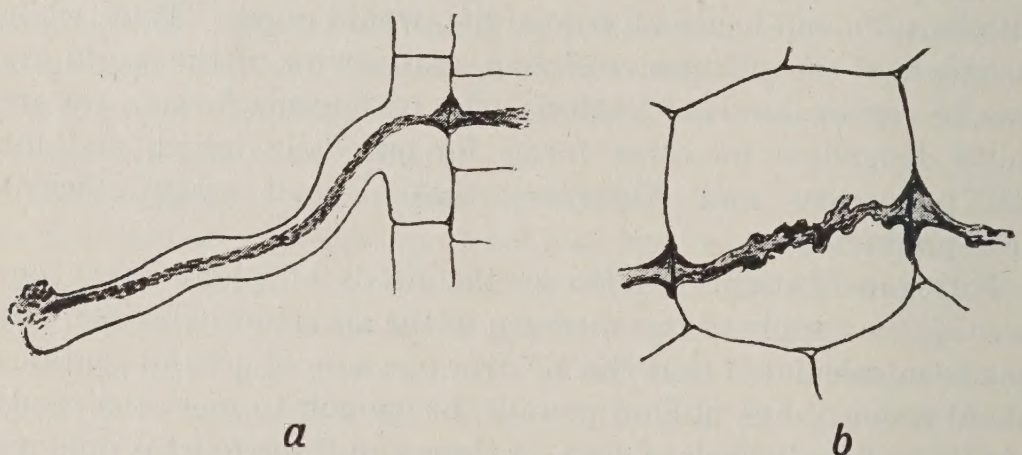


FIG. 138.—*a*, Infection thread of root-tubercle bacillus (*Bacillus radicicola*) entering the root-hair of a pea plant. *b*, Infection thread passing through a cell of a young nodule. (After Percival.)

appear X- or Y-shaped, and sometimes branching even more (Fig. 139). Before their true nature was understood these forms were commonly referred to as "bacteroids," but now that they are known to be true bacteria the term bacteriods (bacteria-like) is being abandoned. By the experiment of growing legumes in soil thoroughly sterilized so as to kill all bacterial life, it has been

[1] Pure cultures of this organism were first isolated in 1888 by Beijerinck, who obtained rod-shaped forms and "swarmers" measuring only 0.9μ long and 0.18μ wide. (A μ—Greek, mū, = 0.001 mm.). Golding found that the swarmers would pass through the pores of a porcelain filter. They are among the smallest living things.

[2] These nodules are variously referred to as *leguminous tubercles*, root-tubercles, and root-nodules. Hellriegel and Wilfarth (1886 and 1888) were the first to show that legumes derive their nitrogen from the air, and that this is accomplished only by the organisms causing the root-tubercles.

found that no tubercles develop in the absence of *Bacillus radicicola.*

According to recent studies of Löhnis and Hansen[1] there are two groups of bacteria that form nodules on the roots of legumes. The first group comprises those organisms having all the specific characters of *Bacillus radicicola,* described by Beijerinck. They produce the nodules on roots of clover (Fig. 8), sweet clover, alfalfa, vetch, pea, navy bean, lupine, black locust, false indigo (*Amorpha*), and the wild beans (*Strophostyles*). In this group

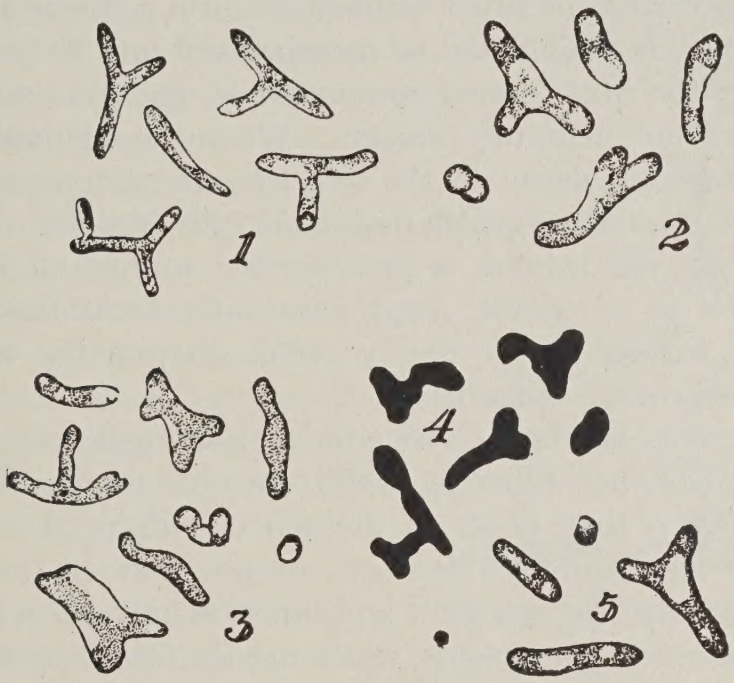


FIG. 139.—*Bacillus* (*Pseudomonas*) *radicicola.* 1, From sweet clover (*Melilotus alba*); 2 and 3, from alfalfa (*Medicago sativa*); 4, from hairy vetch (*Vicia villosa*). (After Harrison and Barlow from Lipman.)

the flagella (by which they move) occur over the whole body (*peritrichic*). They grow comparatively fast in cultures on agar, and produce certain characteristic changes in milk.

The second group are *monotrichic,* that is, they have but one flagellum at the end of the body. They grow more slowly than those of the first group on agar plates, and do not produce the characteristic alteration of milk. They have been isolated from cowpea, soybean, peanut (Fig. 255), beggarweed (*Desmodium*

[1] Löhnis, F. and Ray Hansen. Nodule bacteria of leguminous plants. Jour. Agr. Res. **20**: 543–555. Jan. 3, 1921.

tortuosum), *Acacia*, *Cassia*, and *Genista*. The life histories of these organisms are not sufficiently well known to enable one to say whether they are distinct species or only different forms of the same species.

In the case of each group, the leguminous plant harbors the organism, and furnishes it with carbohydrates and other necessary substances for its nutrition. By breaking down the carbohydrates into simpler compounds the bacillus obtains the energy required to "fix" the free atmospheric nitrogen, *i.e.*, to cause it to unite with some other element to form a nitrogenous compound, which is assimilated or incorporated into its own tissues. Just what the first formed compound is, and the steps in the process are not definitely known. When the leguminous roots and the bacteria decay in the soil, the nitrogenous compounds are set free, and thus furnish material for the process of nitrification. While the legume is growing the compound formed in the nodules is, of course, being constantly translocated to the stem and leaves, and is finally removed from the field when the legume is harvested as hay.

Experiments of Maze,[1] and later of Beijerinck,[2] and Chester[3] demonstrated that tubercle bacilli are able to fix atmospheric nitrogen when they occur in the soil outside of the tubercles. But since they are *anaerobes* (*i.e.*, cannot grow in the presence of free oxygen) they can grow and function only when associated with other aerobic organisms, which use the free oxygen so vigorously as to produce an essentially anaerobic environment for the nitrogen fixers. These anaerobic conditions are realized best and most naturally within the tubercles, where, as Lipman demonstrated, the organisms show much greater nitrogen-fixing power.

A quantitative expression of the value of these nodule-inhabiting organisms was obtained by experiments in 1907 at the Michigan Agricultural Experiment Station, where soybeans with nodules on their roots were found to yield 113.55 lbs. of nitrogen to the acre, while those without nodules yielded only 75.98 lbs.—more than 50% increase with nodules; for cowpeas the figures were

[1] Maze. Ann. de l'Inst. Pasteur **11**: 44–54. 1897.
[2] Beijerinck. Centralblatt f. Baketeriologie **12**: 687. 1892.
[3] Chester, F. D. Delaware Coll. Agr. Epx. Sta. Bull. 66. 1904.

139.21 and 118.45 respectively—an increase of over 17% with nodules (Cf. Fig. 140).

Legumes and Reforestation.—In 1912 a severe fire occurred following logging operations in the Stanislaus (California) National Forest. Vegetation reclaimed the ground slowly, but finally on an area of about three-quarters of an acre of the burned ground the lupine (*Lupinus Grayii*) became very abundant, making a continuous ground cover. Seedling trees began to appear on this area in much larger numbers than on adjacent areas having similar soil and exposure, but no stand of lupine. During the fourth year these trees began to grow noticeably faster than those not surrounded by lupines, and at the end of the eighth year (1920) they were nearly two feet taller than the other trees. Munns[1] attributes the difference to the increased nitrates formed in the soil by the leguminous-tubercle bacilli on the roots of the lupines.

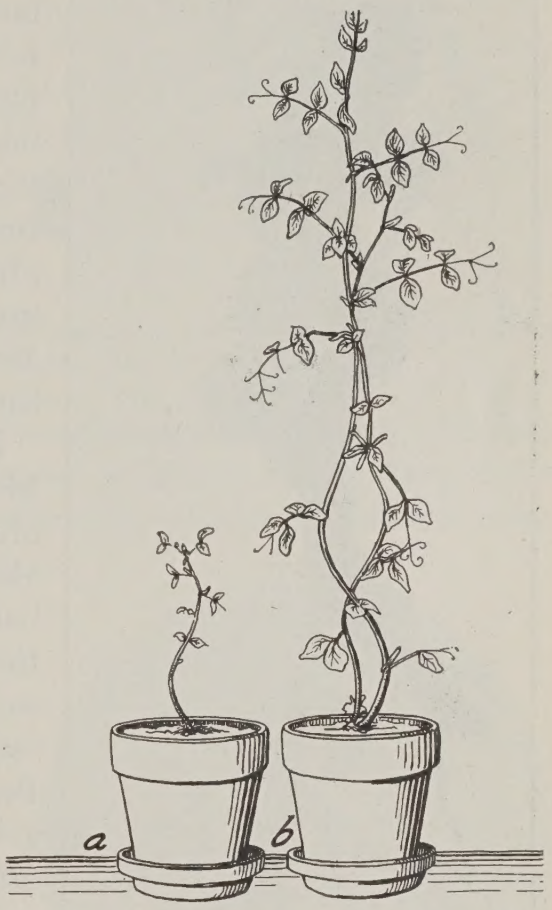


FIG. 140.—Two plants of the edible pea which were grown in clear quartz sand, watered with a nutrient solution containing all necessary nutrients *except nitrogen*. The conditions were identical, except that the left-hand plant had no root-tubercles, while the right-hand plant had numerous well-developed tubercles. (Redrawn from Marshall, Michigan Agr. Exp. Sta.)

Nitrogen-fixation by Molds and Bacteria.—The ability to fix atmospheric nitrogen is possessed by several other species of bacteria, and also by some molds. Recent experiments by Wann[2] have shown that seven species of green algae (Chlorophyceae), when grown on agar and supplied with ammonium nitrate and calcium nitrate

[1] Munns, E. N. Reproduction and nitrogen. Jour. Forestry **20**: 497–498. May, 1922.

[2] Science N. S. **51**: 257–258. March 5, 1920.

in measured amounts, in the presence of glucose, can utilize or fix free nitrogen.[1]

Melvin[2] found that pine seedlings two years old cultivated under sterile conditions, without being supplied with any of the salts of nitrogen, developed satisfactorily, if the soil was inoculated with mycorrhizal fungus from a pure culture; otherwise the seedlings perished. This indicates that, while experiments showed that this fungus does not fix free atmospheric nitrogen in pure cultures, it can do so when growing as an ectotrophic mycorrhiza on the roots or conifers. (*Cf.*, p. 214.)

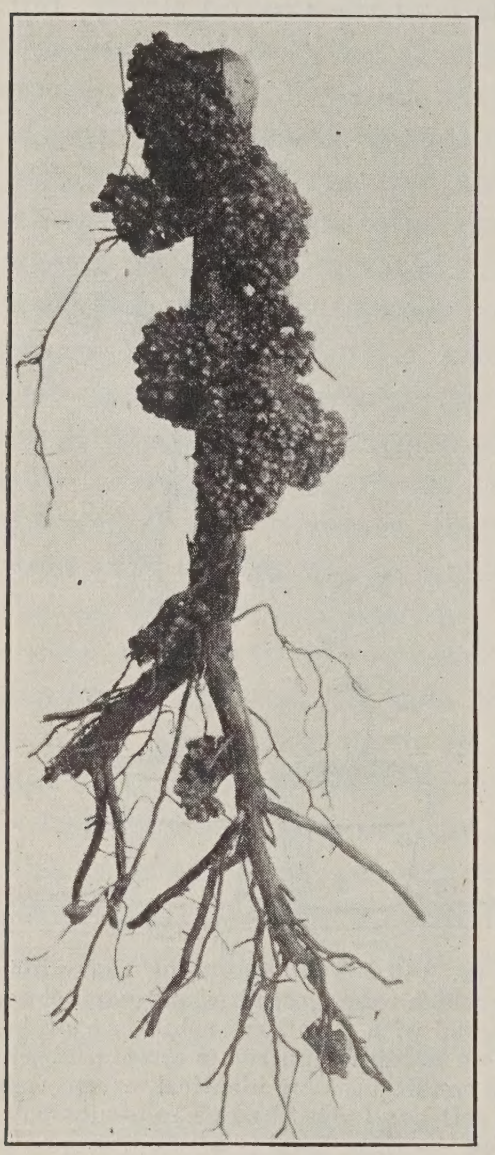


FIG. 141.—Root-tubercles on a species of silverberry (*Elaeagnus*).

Non-leguminous Nodules.—Moreover, root-nodules caused by nitrogen-fixing organisms, occur also on the roots of certain plants belonging to other families than the pea family (Leguminosae), such, for example, as the Oleaster family (*Elaeagnaceae*, Fig. 141), Bayberry family (*Myricaceae*), the genus Alder (*Alnus*) of the Birch family (*Betulaceae*), the Podocarpineae (a tropical or subtropical family), the Cycads (Cycadaceae), and other Gymnosperms (*Pinus*, *Picea*, *Abies balsamea*). The roots of *Cycas* contain two kinds of nitrogen-fixing organisms, *Pseudomonas radicicola* and *Azotobacter*

[1] Moore, Whitley, and Webster found that the green alga, *Enteromorpha compressa*, in sunlight, assimilates more nitrogen than occurs as ammonia, nitrate, or nitrite in the sea-water in which the alga is immersed. From this they infer that the plant fixes nitrogen (as well as CO_2) from the air. Proc. Royal Society. B. **92**: 51–60. 1921.

[2] Melvin, Elias. On the mycorrhizas of *Pinus sylvestris* L. and *Picea Abies* Karst. Jour. Ecol. **9**:254–257. Feb., 1922.

(Fig. 143). The latter are relatively large bacilli and can live only when supplied with oxygen (*aerobic*). They also exist free in the soil.

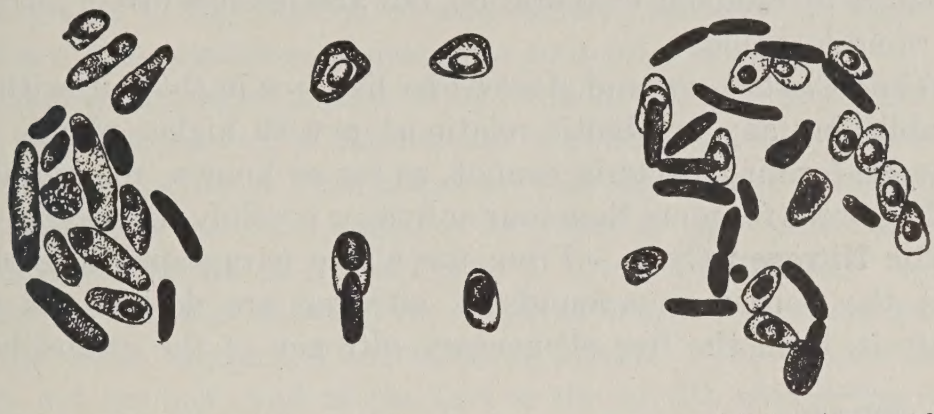


FIG. 142.—*Clostridium* (*Bacillus*) *pasteurianum*, a non-symbiotic nitrogen-fixing organism. (After Winogradsky from Lipman.)

A third type, *Clostridium Pasteurianum* (Fig. 142), first isolated by Winogradsky, can live free in the soil and multiply in the absence of free oxygen (*anaerobically*). It may flourish in compact, fine-grained, poorly aerated soil, while the species of *Azotobacter* (Fig. 143) thrive chiefly in lighter, well aerated soils. All of these forms of soil bacteria must have food as well as nitrogen, and this may be supplied by the organic matter of the manure and other fertilizer commonly applied to soil. Obviously, nitrogen-fixation will proceed most vigorously in a well fertilized soil. With these facts in mind we can appreciate the terse statement of Chester: "Humus, lime, tillage, are the three words that should be kept continually in mind if we would increase the productivity of our lands." Humus and soil treatment, including the application of limestone and phosphorus, and the plowing-in of clover, alfalfa, or other legumes, are probably the most important factors of the

FIG. 143.—*Azotobacter vinelandii* (×1000), a non-symbiotic nitrogen-fixing organism. (From Lipman's "Bacteria in Relation to Country Life." Copyright 1908 by The Macmillan Co. Reproduced by permission.)

three. Under tillage, plowing insures thorough aeration and mixing of the soil, cultivation conserves nitrates by preventing weeds from using them, and mulching not only conserves soil moisture by reducing evaporation, but also reduces loss of nitrates by rapid leaching.

While *Clostridium* and *Azotobacter* live free in the soil, without establishing any symbiotic relationship with higher plants, the tubercle-forming bacteria cannot, so far as known, remain alive and vigorous for more than four or five, or possibly six years.

The Nitrogen Cycle.—From the above paragraphs it is clear that the various compounds of nitrogen are derived, in last analysis, from the free elementary nitrogen of the atmosphere.

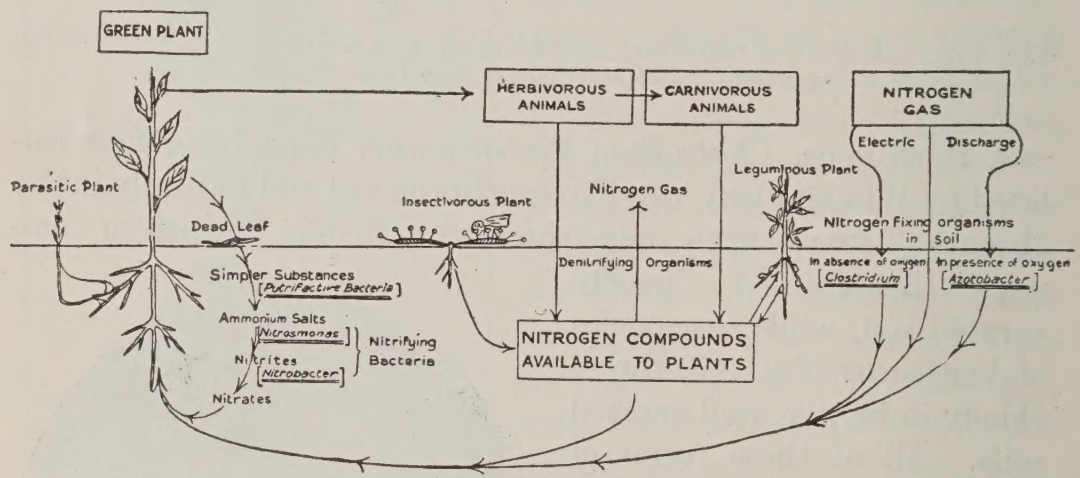


FIG. 144.—Diagram to illustrate the circulation of nitrogen in nature. (After Jones and Rayner.)

After being incorporated in the more complex nitrogenous compounds of plants and animals such, for example, as protein, the nitrogen is ultimately set free and returned to the atmosphere from which it came, completing a round of changes known as the *nitrogen cycle.* (Fig. 144.)

The Necessity of Leguminous Crops.—We are now in a position to appreciate the agricultural significance of leguminous crops. Without them it would not be possible to maintain the fertility of the soil. When such crops are harvested the roots, with their tubercles rich in nitrates and other compounds of nitrogen, are left in the soil. These compounds are dissolved in the soil-water and become available to the next (non-leguminous) crop, such as wheat or potatoes. The value of crop-rotation has been recog-

nized from very early times, but the reason or advantage of including a leguminous crop in the rotation was not understood until as recently as 1889, when Hellriegel discovered the rôle of such plants in the fixation of atmospheric nitrogen through the action of the organisms causing the root tubercles.[1]

Experiments were carried on by Scofield[2] from 1912 to 1920 to test the effect of two or three years of alfalfa in a rotation on the subsequent yields of Irish potatoes, oats, and sugar beets grown under irrigation over a period of six years at three different stations in the northern Great Plains of the United States. Comparison was made between the yields of these crops when grown in the same sequence, but without alfalfa. The alfalfa crops were cut for hay, and at the end of the alfalfa period the land was plowed soon after the last cutting, so that only the stubble was plowed under. The results varied with the type of soil—whether sandy loam or clay loam. At Scottsbluff, Nebraska, with light clay loam, the effect of the alfalfa was to increase the yield of potatoes about 100 bushels per acre, to increase the proportion of marketable potatoes about 12 per cent., to increase the yield of oats about 6 bushels per acre, and to increase the yield of sugar beets 3.4 tons per acre. At Scottsbluff the alfalfa was found more beneficial than farm manure, but with other crops and at other stations the farm manure, in general, gave better results. However, of the positive advantage of including alfalfa in the rotation there can be no doubt.

Inoculation of Soils.—When the farmers of New England and other eastern regions migrated west and began to place the virgin soil under cultivation they soon found that in certain regions of the "Middle West," and notably on the prairies of Illinois and adjacent states, it was difficult, if not impossible, to raise clover; it was first necessary to get a "catch," as they called it. After the first "catch" the succeeding crops gave larger and larger yields. They thought it was necessary to get something (which

[1] Hellriegel, H. Welche Stickstoffquellen stehen der Pflanze zu Gebote? Tagebl. 59 Versamml. Deut. Naturf. u. Aerzte (Berlin) 1886, p. 290; and Landw. Versuchs Stationen **33**: 464–465. 1886.

Hellriegel and Wilfarth. Erfolgt die Assimilation des freien Stickstoffs durch die Leguminosen unter Mitwirkung Niederer Organismen. Ber. Deut. Bot. Ges. **7**: 138–143. 1889.

[2] U. S. Dept. Agr. Bull. 881. Washington, D. C., Aug. 10, 1920.

they called the "wild nature") *out* of the land.[1] In the light of our knowledge of nitrogen fixation it is now known, of course, that, on the contrary, it was necessary to get something *into* the land, and that something was the tubercle bacilli. In one case, after a rotation of timothy, oats, and corn for over six years, the first attempt to grow clover resulted in total failure. There was somewhat better success the second year, but not a large enough crop to harvest; the third year there was "an excellent catch." The reason why clover will not succeed on acid soils is that the tubercle organism cannot live in an acid environment; hence, also, the advantage of liming the soil. It has been found possible to inoculate a field with these organisms by collecting the upper two or three inches of soil where clover grows well and scattering it over the field where clover does not thrive.[2] An important disadvantage of this practice, however, is that weed seeds, and often organisms causing plant diseases, may thus be widely distributed. Numerous instances are on record of this. Similar results have also been obtained by scattering clover straw and chaff. Fields have also been known to become well inoculated by the drainage water from an adjacent and more elevated field.

Commercial Preparations. *a. Alinit.*—Various so-called "germ fertilizers" for inoculating soil with nitrogen-fixing organisms, have been placed upon the market. Several years ago *alinit* was widely advertised, but the results following its use were disappointing. The germ element in this preparation was the spores of *Bacillus ellenbachiensis,* but extensive and careful analyses of soils by Chester revealed the fact that this organism was present in every sample examined. The inference seemed justified that it is of nearly universal distribution and that, therefore, its artificial application was of slight, if any, value.

[1] Hopkins, C. G. Univ. Illinois Agr. Exp. Sta. Bull. 94. 3rd Ed., 1910.

[2] About 200–500 lbs. of soil per acre are commonly used. The broadcasting should be done on a cloudy day with little wind. The only sure way to tell whether soil contains the bacteria necessary for a given crop (except by pure cultures in the laboratory) is to grow some of the plants in the soil and then observe whether nodules are formed on their roots. It has been suggested that water used in irrigation may also carry nodule forming bacteria, and the growing of legumes on the banks of irrigation ditches has been recommended as a means of supplying the bacteria to the water.

b. Nitragin.—Pure cultures of tubercle organisms of different kinds have been sold under the names *Nitragin* and *Nitrobacterine.* These cultures, on moist nutrient media, were intended to be mixed with seed or scattered over the soil of a field supposed to be deficient in these organisms, but their use has not given as satisfactory results as the application of soil from other fields rich in the bacteria, or as the raising of some legume for two or three successive seasons.

c. Pure Cultures.—About 1904 the U. S. Department of Agriculture began to distribute pure cultures of *Bacillus radicicola* dried upon cotton wool. Obviously, the success of such preparations would depend upon the ability of these bacteria to withstand dessication. While there was some evidence that inoculation with these cultures was beneficial, careful and repeated experiments at several State Experiment Stations demonstrated conclusively that the organism does not long remain active when dried, and quickly dies when exposed to the air on cotton. This method of inoculation is no longer advocated.

Legume Inoculation.—As stated above, the nodules on each species of legume are, in general, caused by a different form of bacterium. Clover bacteria will not inoculate peas or beans, alfalfa bacteria will not inoculate red or white clover nor alsike. Recent work has shown that the legumes fall naturally into about a dozen different groups, the species in each group having their root-nodules produced by the same species of bacterium. Cross-inoculation by scattering soil must, therefore, be carried on within a given group. Thus, for example, garden and field peas, vetch, and sweet peas are all in the same group. Fortunately for agriculture and the farmer, common and yellow-flowered alfalfa, white and yellow sweet clover, and yellow trefoil are in one group. Nodule bacteria of lima beans (*Phaseolus lunatus*) are the same as those of the cowpea (*Vigna Catjang*), but different from those of navy and kidney beans (*Phaseolus vulgaris*).[1] But soil inoculation will not insure a good crop unless the other conditions of soil and climate also favor the crop.

Inoculation of Non-legumes.—Numerous attempts have been made (by Burrill and others) to inoculate the roots of corn

[1] This whole question is still not well understood, and there is need of much additional investigation.

(*Zea Mays*) and other non-leguminous crops with nitrogen-fixing organisms, but so far without success. If such a result could be obtained its great advantage to agriculture is obvious.

Other Micro-organisms in the Soil.—Although the soil has been cultivated by mankind for untold ages—from prehistoric times—there has probably been no substance playing so intimate and necessary a part in our daily lives and so little understood. Until within the memory of men now living it had always been supposed that the soil, in its relation to crop-production, was composed of non-living matter, and that the processes taking place within it were purely physical and chemical. In fact, the study of the soil has, until the past few decades, been left to chemists and physicists. But, with the advent of the new science of bacteriology, the study and interpretation of soils became revolutionized. In addition to the macroscopic forms of animal and plant life, and microscopic animals, the soil is a veritable botanic garden of micro-organisms, including yeast, molds, diatoms, and algae, as well as innumerable kinds of bacteria. The number of individual organisms staggers our imagination. The number of bacteria alone in one gram of the first six or eight inches of arable soil has been estimated at from 300,000 to 5,000,000. The estimate for a black peaty soil in Russia was 60,000,000 per gram. In addition to these forms there are the innumerable mycelial filaments of the mushrooms and other fleshy fungi, and the seeds, roots, bulbs, underground stems, *et cetera* of the higher plants. The change in our knowledge of the soil, as a result of modern studies, is tersely reflected in the now current phrase "*the living soil.*"

CHAPTER XIII

GROWTH

Definition.—*Growth is increase in size* of either the organism as a whole or of any of its parts. By growth the individual protoplast of a cell may become more bulky, the chloroplasts or leucoplasts may become larger, the nucleus bigger, the cell-walls thicker, the cell as a whole may increase in any dimension, and, as a result of this, the tissues and organs, and finally the entire organism, may become larger. Growth does not always involve the whole organism. Cell-walls often grow thicker while the size of the plant as a whole does not alter. Growth often involves a decrease in the size of one or more of the parts; thus, when a potato "sprouts," the tuber itself, giving its substance to nourish the newly formed stems, becomes smaller and lighter in weight, while the stems increase in size and weight. As a whole, however, the potato plant is growing (Fig. 109).[1]

Osmosis and Growth.—Growth does not always involve increase in weight. If, for example, the pressure resulting from osmosis increases within a turgid cell, and if the cell-walls are elastic, the cell will grow bigger in one or more dimensions. Not only may this growth involve no increase in weight (as, for example, when an increase of pressure within a cell results from the changing of starch to sugar), but may even be accompanied by loss of weight on account of waste products being given off by the growing cell. It has been generally considered that osmosis is the most important immediate cause of increase in size of nearly all tissues and organs, but recent investigations by MacDougal on the physical factors involved in the growth of the tomato fruit indicate that, in the growth of young fruits, the chief distentive force is the imbibition of water by the cell-walls and

[1] The term growth is variously defined by different physiologists. Here, as always, one may adopt any rational definition, provided the term is always used in the same sense throughout the same discussion.

the colloidal cell-contents. Osmosis may play a more important part in a later stage of growth. The result is a structure like the tomato (and other fruits of the berry type, and also fruits like the melons) having from 97–98% water and only 2–3% solid matter. This is the reverse of the manner of growth common in other and non-succulent parts (*e.g.*, seeds, tubers, woody stems, and leaves) in which the percentage of dry substance is least in the early stages of growth and greatest at maturity.

The great amount of force often exerted by young growing organs, due to the pressure within their cells, is strikingly illus-

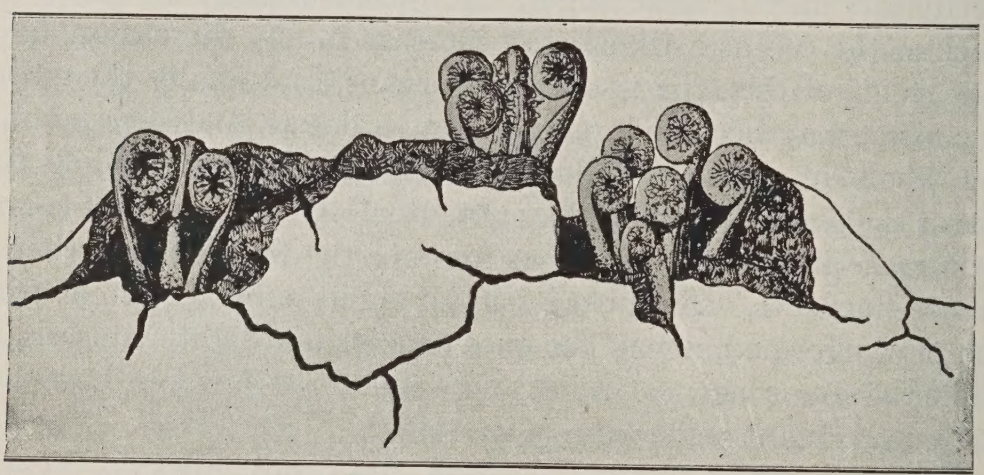


FIG. 145.—The rupturing of concrete by the growth of young leaves of the ostrich fern (*Onoclea Struthiopteris*). (After Stone.)

trated in Fig. 145, showing the rupturing of a concrete pavement by young fern leaves.

Experiment in Growth.—The relation between osmosis and growth may be demonstrated by a very simple experiment, illustrated in Fig. 146. *P* is a portion of the herbaceous stem of any convenient plant, fastened securely at one end to an iron clamp (*C*), lying at the bottom of a glass jar (*J*). The upper end of the stem is attached by a small thread to the short arm of an index (*I*), the opposite end of which may move up and down over a graduated scale (*S*). If the jar is filled with a solution of common salt in water, water will pass out of the plant tissue by exosmosis. This will reduce the pressure (*turgor*) within, and the stem will shorten, on account of the contraction of the elastic cell-walls, causing the long arm of the index to move up over

the graduated scale. If the salt-solution is now removed, and the jar filled with tap water, or better, distilled water, the water will enter the cells of the stem by osmosis, increasing the internal pressure and turgor of each cell. As a result the stem as a whole will elongate or grow in length, thereby causing the index to move down over the scale.

Differential Growth.—Not all the tissues of a stem or other part grow at the same rate.[1] On this account, and since adjacent tissues are closely united, those which elongate or grow more slowly are stretched by those which grow more rapidly. As a result either a state of tension exists, or the organ is distorted,

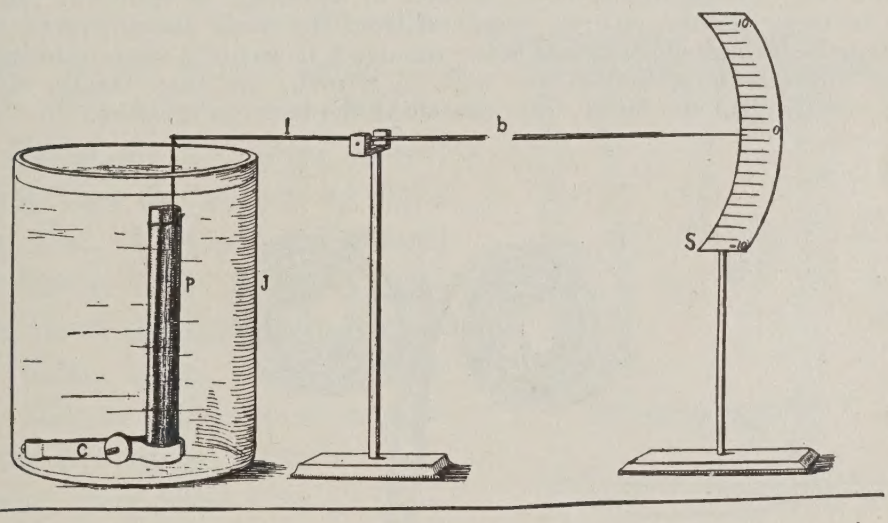


FIG. 146.—Experiment to demonstrate the relation between osmosis and growth in length. *J*, jar containing water, and subsequently salt-solution; *p*, portion of leaf-stalk of Rhubarb; *I*, index-lever (portion omitted at *b*); *S*, scale. Explanation in text.

or both. When one epidermis of a leaf grows more rapidly than the other, distortion results, and the leaf becomes "crisped" or crinkled. This is normally the case in some plants, but in others the crisping may denote a diseased condition of the leaf.

Tissue-tension.—If a thin surface strip of tissue is cut away for a short distance from a stalk of celery, or thick petiole of a burdock or other leaf, the strip at once curves outward, on account of its *longitudinal tissue tension.* We are all familiar with this phenomenon (Figs. 147 and 148). When boys make whistles from young willow twigs in spring, a cylinder of bark is removed, and may be easily replaced; but if the cylinder of bark

[1] The student should endeavor to reason out an explanation for this.

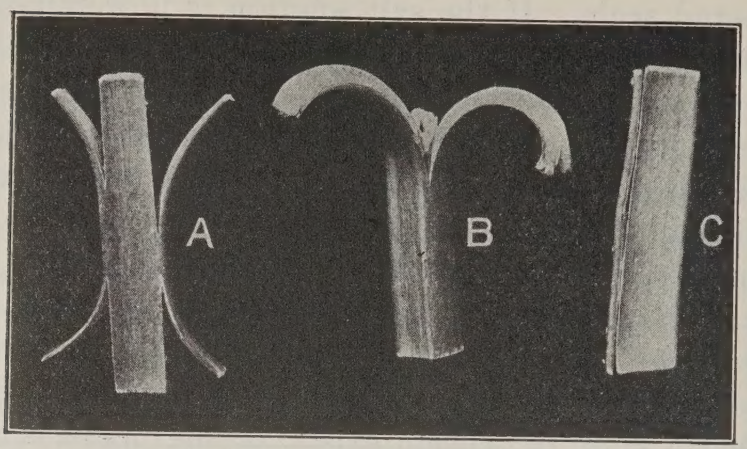


FIG. 147.—Longitudinal tissue-tension in leaf-stalk of rhubarb. In C the strip of outer tissues, entirely removed from the main piece, is seen to have shortened, showing that, before being removed, it was in a state of longitudinal tissue-tension, owing to the fact that, in growth, the inner tissues elongated more rapidly than the outer, thus stretching the latter lengthwise.

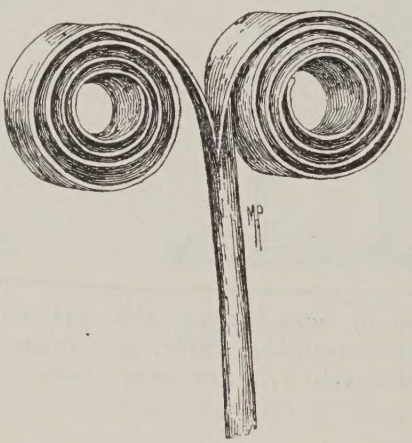


FIG. 148.—Portion of dandelion scape, showing "curls" resulting from longitudinal tissue-tension.

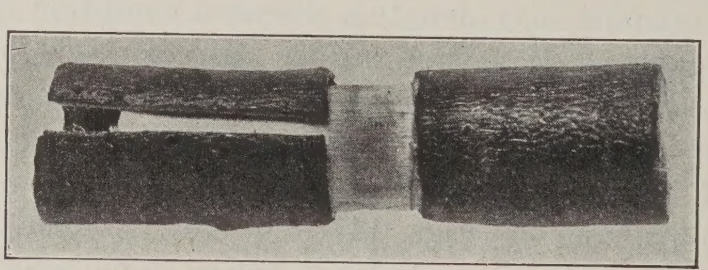


FIG. 149.—Portion of stem of a willow, illustrating transverse tissue-tension. By gentle tapping and twisting, the cambium layer has been bruised, so that a small cylinder of the bark was easily twisted off.

becomes split lengthwise, the edges cannot be made to come together around the wood without considerable stretching. This illustrates *transverse tissue-tension* (Fig. 149). If the preceding statements in this chapter have been understood, the student should now be able to explain these phenomena without further assistance.

Elongation of Roots.—In order to ascertain the manner of growth of roots, the root of a young seedling of lupine, or other plant, may be carefully marked with dots or lines of India ink, at intervals of 1 millimeter, beginning about 1 millimeter back from the root-tip, and extending for a distance of 15 to 20 millimeters. If the root is again observed, after having been left to grow for about 24 hours, it will be found that the first six or eight marks near the tip have spread apart, those from 3 to 7 millimeters from the tip having separated more than those farther back. Those marks most remote from the tip will be found to have separated very little if at all (Fig. 150). By this simple experiment we learn that the growth in length of roots is largely confined to a zone a few millimeters in length directly back of the root-tip. It should also be noted in this connection that the zone of root-hairs begins just back of the zone of growth, no root-hairs being found in the region of elongation.

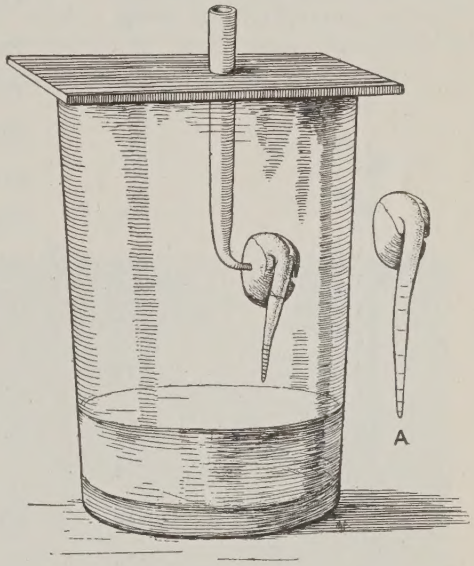


FIG. 150.—Experiment to show the method of growth in length of a root. *A*, 24 hours after the condition shown in the glass.

Elongation of Stems.—The manner of elongation of stems may be ascertained by marking the internodes[1] of a young growing stem throughout their entire length. Two or three adjacent internodes near the tip of the stem should be marked. After a period of from 24 to 36 hours the marks will be found to have separated, but, in contrast to the behavior of the root, the marks will be found to have separated through the entire extent of the internode, and several adjacent internodes will be

[1] An internode is the space between two successive leaves on the stem.

found to have elongated at the same time (Fig. 151). This contributes to the more rapid elongation of the stem, and is an advantage to the plant, since the leaves are thereby more rapidly brought into positions of best exposure to air and sunlight. The growth of several internodes at the same time, and their elongation throughout their entire length, carries the tip of the stem forward more rapidly than if growth were confined to a short zone, as in the case of the growing root. But a more rapid and forceful advance of the root-tip through the soil might result in serious or fatal injury, on account of the resistance and obstacles encountered in the soil. Thus the different manner of growth of stems and roots is seen to be of direct advantage to the plant as a whole.

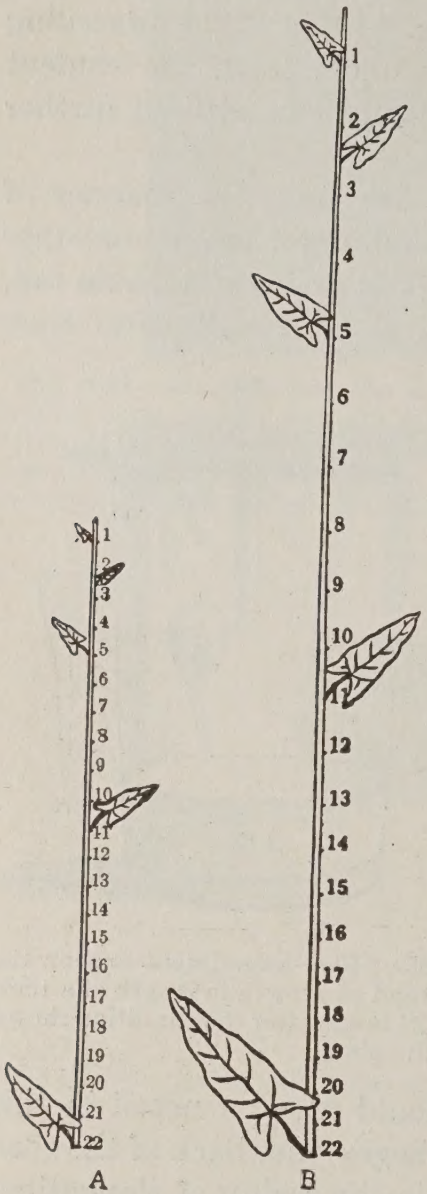


FIG. 151.—Diagram showing mode of growth in length of a portion of a stem of bindweed (*Convolvulus*). *A*, stem with internodes marked off into intervals of 1 cm.; *B*, the same stem 24 hours later, showing the relative elongation of the various internodes. (Cf. Fig. 150.) (Redrawn from Bonnier and Leclerc du Sablon.)

Growth of Leaves.—In tropical climates leaves that have once begun to form continue to grow until they reach full size; but in temperate climates, having an alternation of summer and winter, this is not the case. Here many of the leaves of any given season are formed during the preceding growing season, and remain over winter in a resting state in buds, ready to expand and become green. The outer coverings or scales of the bud are modified leaves or parts of leaves (Fig. 152). They have almost or entirely lost their character as foliage organs, and while they are forming, their outer (dorsal) surfaces elongate more rapidly than their upper (ventral) surfaces. This causes them to curve

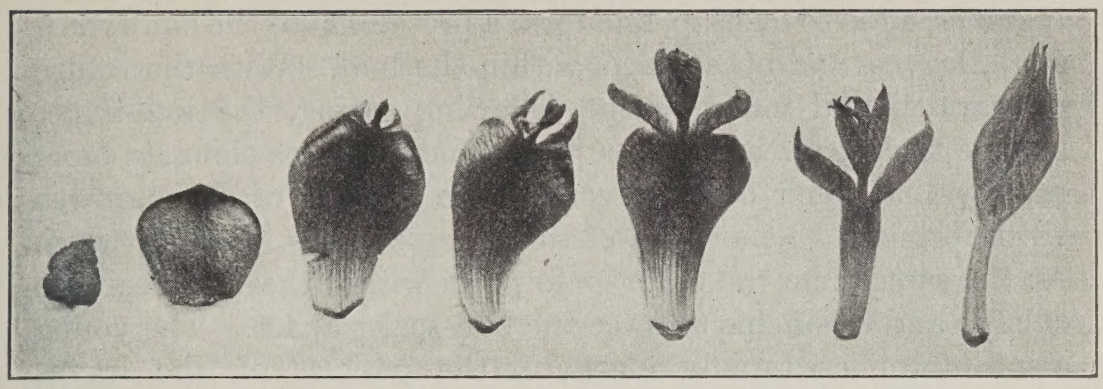


FIG. 152.—Bud scales of an ash showing the gradual transition from the outer scale (at the left) to one of the innermost scales (second from the right), and finally to one of the foliage leaves within the bud. Here the bud-scale appears to represent only the basal part of the leaf-primordium (leaf-base), the primordium of the blade being arrested, and the petiole having failed to develop.

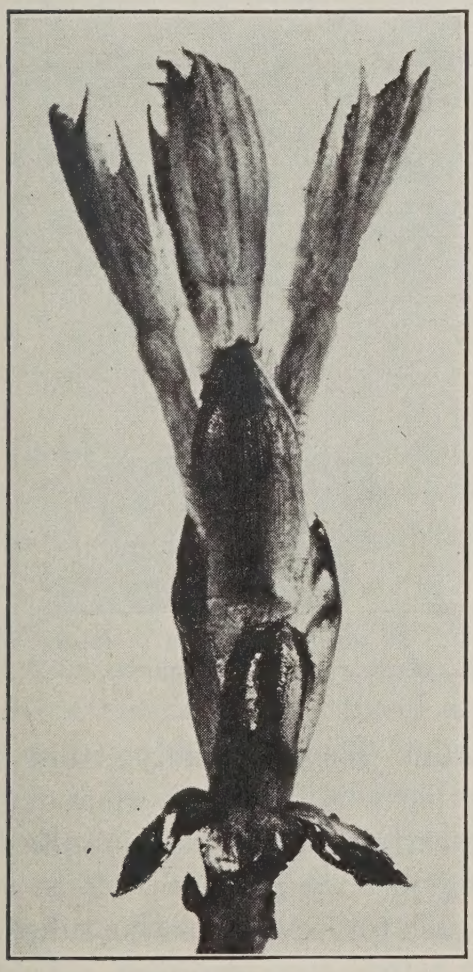


FIG. 153.—Opening buds of a horse-chestnut (*Aesculus Hippocastanum*).

FIG. 154.—Sapling of horse-chestnut (*Aesculus Hippocastanum*), with young leaves not yet wholly expanded.

together, so as to overlap, and form a protection to the embryonic stem, leaves, and other parts within the bud. With the return of warmth and moisture the following spring, the bud-scales resume their growth, but now their inner surfaces elongate more rapidly than their outer, reversing the method of their growth when forming. As a result of this, they begin to open outward. At the same time the embryonic parts within the bud begin to enlarge and this helps to force the bud-scales apart. The young stem-internodes rapidly elongate, the petioles of the leaves increase in length, and gradually the leaf-blades expand as their cells become more and more turgid (Figs. 153 and 154).

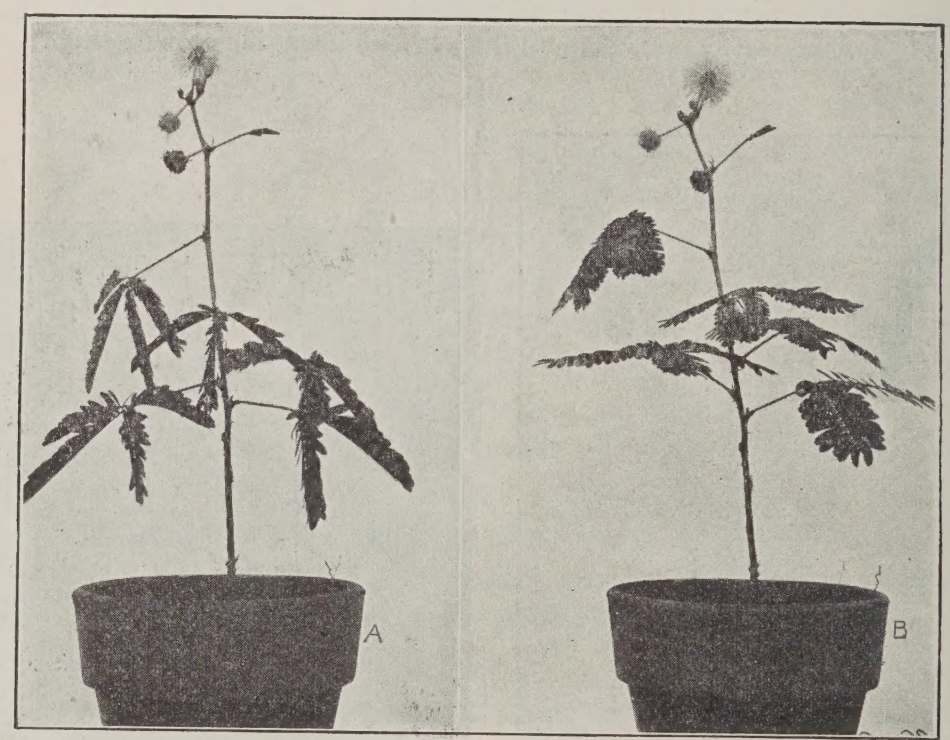


FIG. 155.—Sensitive plant (*Mimosa pudica*). *B*, normal position of foliage in light; *A*, position of foliage after the plant was slightly shaken.

Permanent and Temporary Growth.—The size finally attained by stems, roots, leaves, and other parts is usually permanent; but some growth is temporary, and certain tissues may manifest various alterations in size according to circumstances. This is illustrated by the petals of flowers (such for example as the tulip), that open and close several times before they drop off. This motion is caused by temporary fluctuations of growth of the upper and lower surfaces of the petals. In a similar manner is

explained the change of position of the leaflets of certain plants, such as clover, oxalis, bean, and others, at night or in cloudy weather, and the more rapid motion of the leaves of the Sensitive Plant (*Mimosa pudica*) and other plants (Figs. 155, 156, and 181).

The leaf-movements of the Sensitive Plant, and the so-called "sleep" movements of the leaves of other plants, are due to alterations in the relative turgidity of the tissues of the upper and lower sides of motile organs (*pulvini;* singular, *pulvinus*). These organs are enlargements at the base of the leaves, or of the leaflets, or of both, as the case may be. The change is a response to some stimulus (see p. 285).

FIG. 156.—*Oxalis bupleurifolia*. *p*, Petiole; *b*, trifoliolate blade. At the left, leaflets in normal attitude in light; at the right, attitude of leaflets at night or after sudden shock.

Growth and Nourishment.—When a plant or plant organ is growing, the protoplasm is constantly forming new parts, and therefore must continually be renewed or nourished. The more rapidly new parts are formed, the greater the need for food. This need is provided for in many ways. Young embryos in the seed find a rich supply of nourishment, ready made by the parent plant, stored within their tissues (as in the bean or pea), or around them (as in the corn, or castor-oil seed, Fig. 157). They do not have to manufacture their own food at first. Young and rapidly growing plants (seedlings and young saplings) commonly have much larger leaves than mature plants of the same species (Fig. 102). On this account food making, from the raw materials taken in by the plant, may proceed much more rapidly. Plants commonly store food in quantity where it will be needed in the future by rapidly growing new parts, and such

storage organs usually become swollen by the abundance of stored food. This is illustrated by "potatoes," which, as is well known, are underground branches (*tubers*) stored with food for the use of young sprouts when they begin to grow in the

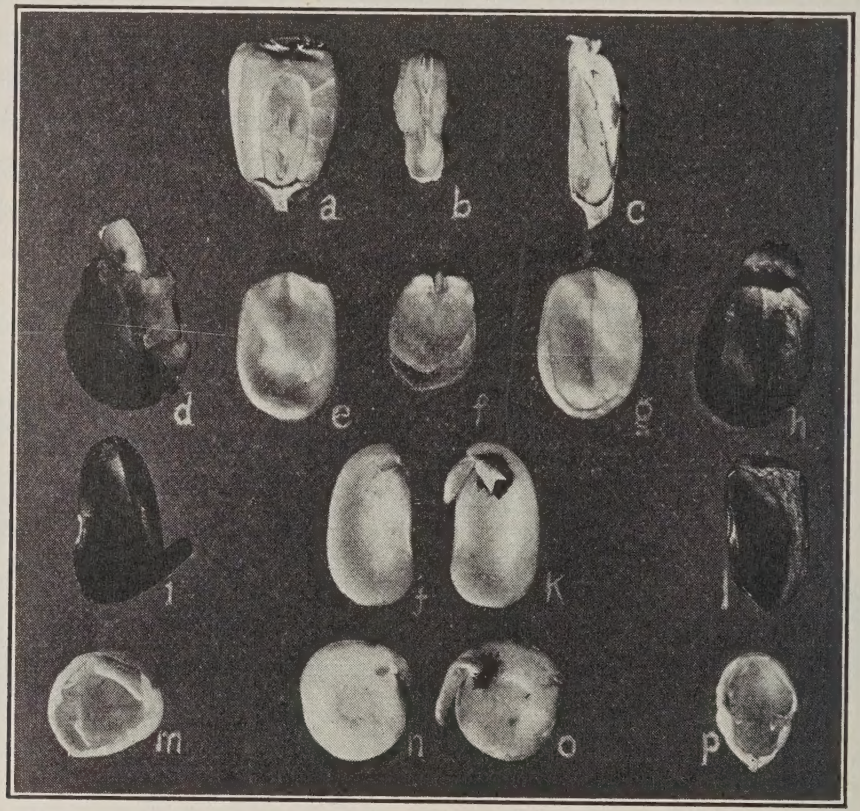


FIG. 157.—*a–c*, Indian corn (*Zea Mays*); *d–h*, Castor-oil plant (*Ricinus*); *i–l*, Bean (*Phaseolus*); *m—p*, Pea (*Pisum*). *a*, surface view with outer skin removed, showing the embryo embedded in the endosperm; *b*, embryo (with one cotyledon) removed from endosperm; *c*, side view of the grain in longitudinal section; *d*, *h*, halves of the seed-coat, with the *caruncle* attached to the right hand half. The lighter areas are portions of the inner, membranous seed-coat (*endopleura*); *e*, *g*, halves of the endosperm which enclosed the embryo; *f*, embryo, with short hypocotyl and two membranous, leaf-like cotyledons; *i*, *l*, halves of seed-coat; *j*, one of the two fleshy cotyledons; *k*, the second fleshy cotyledon, still attached to the hypocotyl, which bears, at its upper end, the plumule, composed of the first two foliage leaves and the enclosed growing point; *m*, *p*, seed-coat; *n*, *o*, same for pea as *j* and *k* are for the bean.

Note that the main axes in the bean and pea are *curved* (nutate), while in the corn and castor-oil plant they are straight. Curved embryos (or straight, as the case may be) are characteristic of entire families of plants. Nourishment, which is stored around and outside of the embryo in corn and castor-oil plant, is, in the bean and pea, stored within the cotyledons of the embryo, hence they are "fleshy."

spring. All bulbs are to be interpreted in the same way. The need on the part of growing plants for an abundance of food is recognized by farmers when they fertilize their fields, thereby

placing in the soil a rich supply of the raw materials out of which the growing crops can manufacture food to meet their needs.

Nutation.—When the organs of plants grow in length they do not elongate at equal rates throughout their entire circumference, or (if flat) on opposite sides, but always grow more rapidly on one side than on the others. This results in the tips of stems and roots bending over to one side; they nod or nutate; the phenomenon is called *nutation*. This method of growth is characteristic of practically all plants, and of all organs—stems,

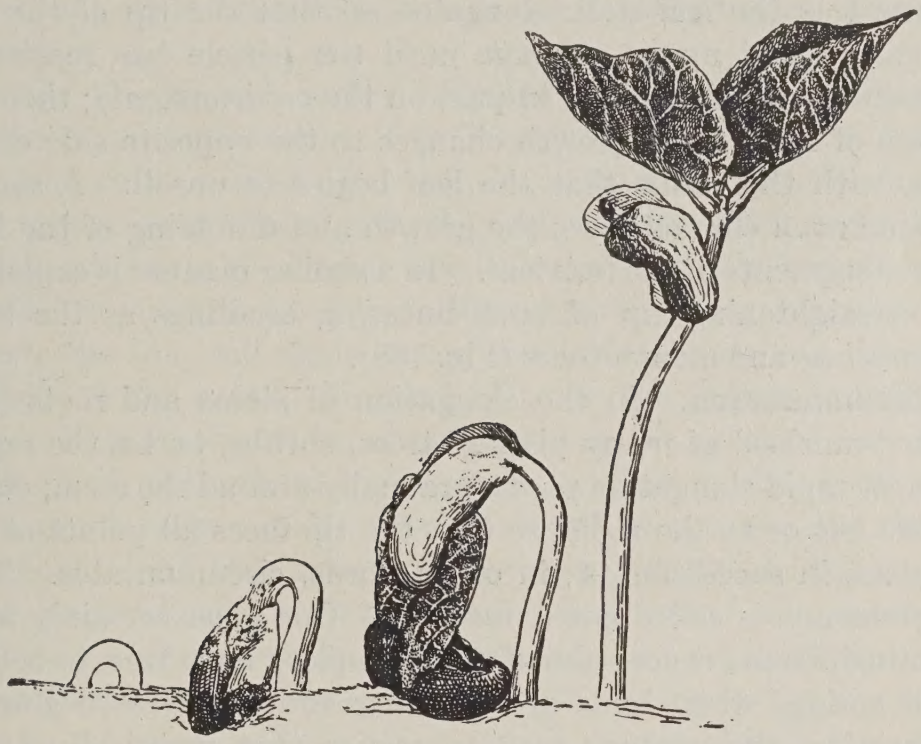


FIG. 158.—Stages in the germination of the common bean (*Phaseolus vulgaris*), showing nutation and hyponasty. (After Atkinson.)

branches, roots, leaf-stalks, midribs of leaves and leaflets, flower-stalks, and modifications of these organs, such, for example, as tendrils.

Nutation may appear in the embryo within a seed (Fig. 157, *k*), in the germinating seedling (Fig. 158), in the growth of a fern frond (Fig. 145), in flower stalks (peduncles and pedicels) (Fig. 423), in the unfolding leaves of cycads, and in numerous other cases. In bud-formation it is the lower side of the scales and leaves that grows more rapidly (*hyponasty*), thus helping to produce the bud, as noted above (p. 250); in the opening bud it is the upper

side of the scales and leaves that grows more rapidly (*epinasty*), thus causing the scales to bend out and the leaves to expand.

Often the region of most rapid elongation may shift more or less abruptly from one side to the other, through 180° of arc, causing the tip of the given organ to nod in the opposite direction. This change may be comparatively frequent, as in the case of the flower stalk of the onion (*Allium*), or it may vary only with the age of the organ or with the season, or a combination of both. In the young fern leaf, for example, the region of nutation travels forward as the leaf-stalk elongates, so that the tip of the leaf remains rolled up or *circinate* until the petiole has reached a certain length (depending in part on the environment); then the region of most rapid growth changes to the opposite side of the axis, with the result that the leaf begins to unroll. A similar phenomenon characterizes the growth and unfolding of the leaflets or segments of the fern leaf. In a similar manner is explained the straightening up of such nutating seedlings as the bean (*Phaseolus*) and many others (Fig. 158).

Circumnutation.—In the elongation of stems and roots (and their branches) of many plants—trees, shrubs, herbs, the region of most rapid elongation passes gradually around the stem, either to the left or to the right, so that the tip faces all points of the compass in succession or, in other words, circumnutates. This phenomenon is called *circumnutation*. One must certainly have a quite different conception of, for example, a large tree, to behold it in spring, when buds are bursting and growth is beginning again after the winter's rest, to realize that practically every free tip, below as well as above ground, is describing a tiny circle or ellipse in space; and this must, above all, be a revelation to those who have held the erroneous idea that one of the ways in which plants differ from animals is that plants have no motion.

It was about one hundred years ago that the first description of circumnutation appeared in the literature of botany. About fifty years later the subject received its most thorough treatment at the hands of Charles Darwin, and we cannot do better than to quote his words here.

"When the shoot of a Hop (*Humulus lupulus*) rises from the ground, the two or three first-formed joints or internodes are straight and remain stationary; but the next-formed, whilst

very young, may be seen to bend to one side and to travel slowly round towards all points of the compass, moving, like the hands of a watch, with the sun. The movement very soon acquires its full ordinary velocity. From seven observations made during August on shoots proceeding from a plant which had been cut down, and on another plant during April, the average rate during hot weather and during the day is 2 hrs. 8 m. for each revolution; and none of the revolutions varied much from this rate. The revolving movement continued as long as the plant continues to grow; but each separate internode, as it becomes old, ceases to move."[1]

"As this movement is rather difficult to understand, it will be well to give an illustration. Take a sapling and bend it to the south, and paint a black line on the convex surface; let the sapling spring up and bend it to the east, and the black line will be seen to run along the lateral face fronting the north; bend it to the north, the black line will be on the concave surface; bend it to the west, the line will again be on the lateral face; and when again bent to the south, the line will be on the original convex surface. Now, instead of bending the sapling, let us suppose that the cells along its northern surface from the base to the tip were to grow much more rapidly than on the three other sides, the whole shoot would then necessarily be bowed to the south; and let the longitudinal growing surface creep round the shoot, deserting by slow degrees the northern side and encroaching on the western side, and so round by the south, by the east, again to the north. In this case the shoot would remain always bowed with the painted line appearing on the several above specified surfaces, and with the point of the shoot successively directed to each point of the compass. In fact, we should have the exact kind of movement performed by the revolving shoots of twining plants."[2]

Climbing.—It is in virtue of circumnutation, combined with growth in length, that twining plants are enabled to twine and to climb by twining. The circumnutation of the tip is of advantage in the first instance in enabling the stem to find a support on

[1] Darwin, C. The movements and habits of climbing plants. Second Ed., Revised, p. 2–3. New York, 1901.

[2] Darwin, l. c., pp. 11–12.

which to climb, and then it enables the stem to twine around the support. Twining plants twine either "clockwise" (to the right) or "counter-clockwise" (to the left), according to the direction of their nutation. Right-handed twiners include the hop (*Humulus*), *Clerodendron*, *Lonicera*, and a few others. The larger

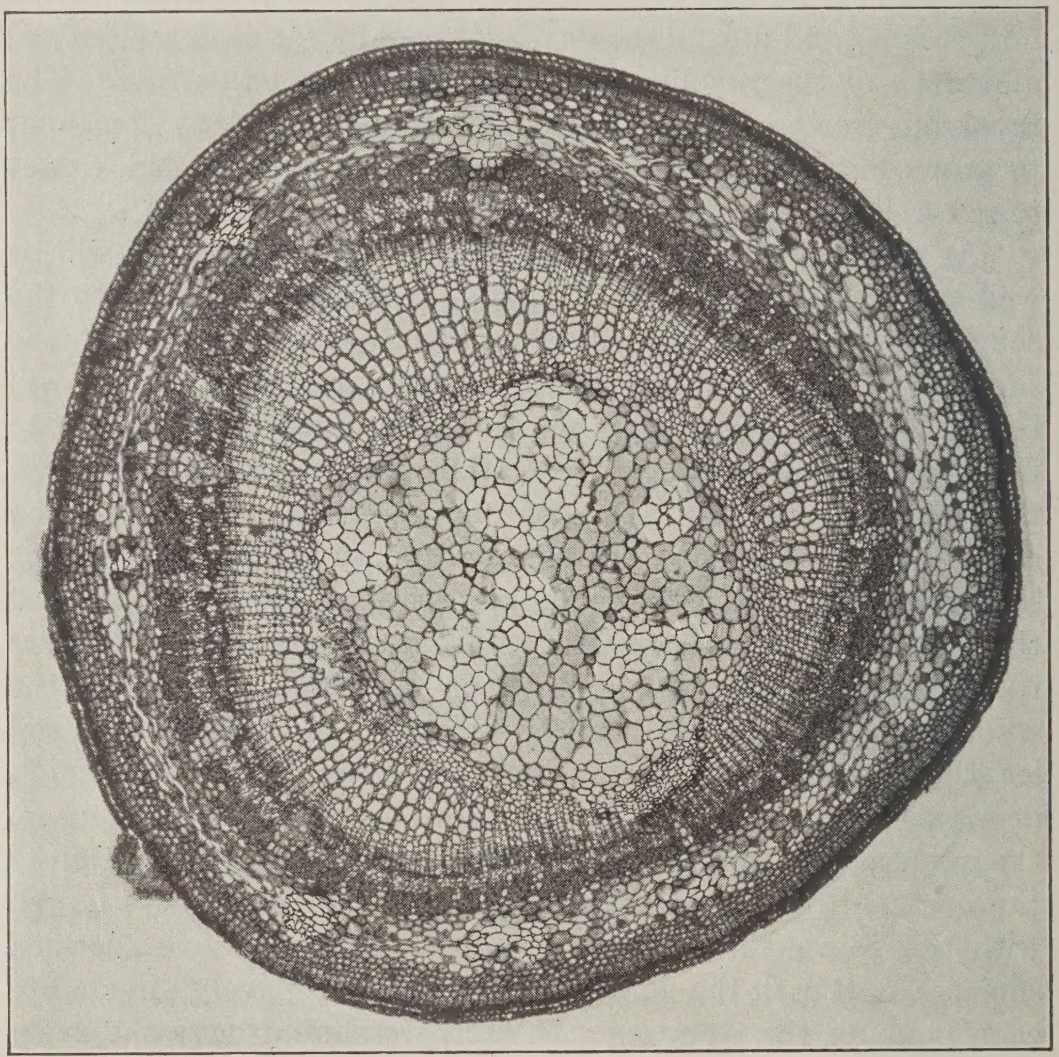


FIG. 159.—Cross-section of a branch of a Linden (*Tilia*) one year old, showing pith in the center, surrounded by one "ring" or layer of wood, outside of which is the young bark with its four regions as described in the text. (Photomicrograph from nature.) Cf. Fig. 160.

number of twiners are left-handed, including, for example, *Aristolochia*, *Tecoma*, the common bean (*Phaseolus vulgaris*), *Asparagus*, and many others.

As is commonly known, there are numerous ways, other than twining, by which plants climb. Some are tendril-climbers, and

the tendrils are commonly sensitive to contact so that they are stimulated to twist around a support when they touch it. Tendrils vary greatly in their morphological significance—that is, in their homology. They may be modified roots (*Vanilla*), branches (grape), leaves (*Bignonia albo-lutea*), leaflets (pea), stipules (greenbrier-*Smilax rotundifolia* ?),[1] or flower-stalks (the bladderwort—*Utricularia reticulata*). In numerous plants (*e.g.*, the nasturtium—*Tropaeolum* sp.) the leaf-stalks act as tendrils (while the blade continues to function in transpiration and photosynthesis), or the tip of the leaf (with the midrib) may be prolonged and serve as a tendril (*Cobaea scandens* and *Gloriosa superba*). There are all gradations between these conditions and that where the entire organ has the structure and function of a tendril. The tendrils of cucumbers, squash, and other cucurbits are modified bracts. In the Virginia Creeper (*Ampelopsis*, or *Psedera*) the tips of the tendrils become modified into adhesive discs when brought in contact with a wall or other support.

Secondary Growth in Thickness of Stems.—When the primary vascular tissue of stems occurs in separate bundles, growth in thickness may proceed, in general, as follows. The fundamental tissue of the primary pith rays, lying between the bundles and on a line with the fascicular cambium, gives rise, by cell-division, to *interfascicular cambium*. By repeated cell-divisions of this tissue new xylem is formed toward the center (next the pith) and new phloem toward the circumference (next the cortex). By

[1] The tendrils of *Smilax* are, as above, commonly cited as examples of stipulate tendrils, but Goebel (*Organography of Plants;* Eng. translation by Balfour, p. 222, etc.) gives several reasons why this interpretation is not correct. They do not, for example, grow out of the leaf-base (as true stipules do), but spring from a point higher up on the leaf. This illustrates what is called *enation* or *emergence*. By this theory it is held that organs may arise as *new formations* at a point previously unoccupied in the race history (phylogeny) of a given species. This theory is in contrast to the theory that there is a definite number of fundamental parts or organs, and that all other organs arise by the transformation or *metamorphosis* of one of the fundamental organs, as when leaf-primordia develop into thorns or into bud-scales, instead of into foliage leaves. The poet Goethe (1790) was the author of a book, *Die Metamorphose der Pflanzen*, in which this theory was elaborated. According to Goebel the tendrils of *Smilax* are new formations, and cannot be referred to (*i.e.*, homologized with) any of the generally recognized parts of a foliage leaf.

further cell-divisions and transformations, during the second year or period of growth, a second layer of xylem (*secondary wood*) is formed just outside the first layer, and a second layer of phloem (*secondary phloem*) just inside the first layer of phloem. In other words, a new cylinder[1] of wood is formed each growing season just outside of and contiguous to the next younger layer. The vascular elements of the layers formed early in the season are of larger diameter than those formed later, causing a rather

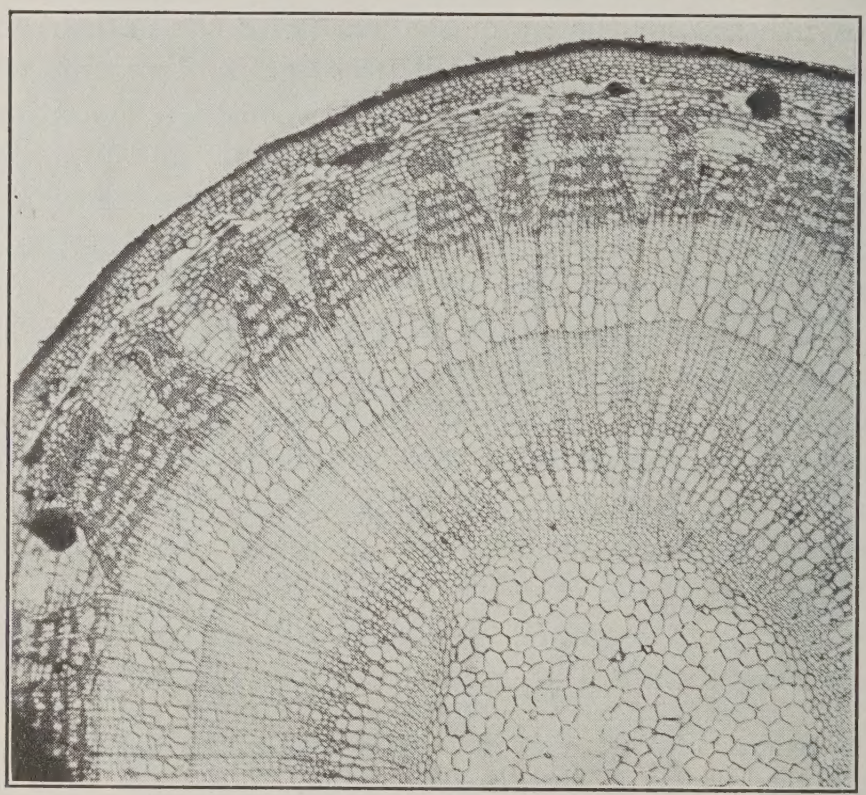


FIG. 160.—Cross-section of a branch of a Linden (*Tilia*), two years old, showing two layers of wood and two of inner bark (phloem). The epidermis is being destroyed by the growth of the branch in diameter. (Photomicrograph from nature.) Cf. Figs. 159 and 44.

sharp contrast where the old and new layers are in contact. This gives rise to an appearance of concentric layers or rings as seen in cross-section (Figs. 159–162.) Since the new layers are commonly formed annually, they are called *annual rings*, and the common belief is that by counting these layers or "rings" one may ascertain the age of the tree or branch. In this connection it should be noted that often more than one layer of new tissue

[1] This "cylinder" is, in reality, a truncate cone. Explain why.

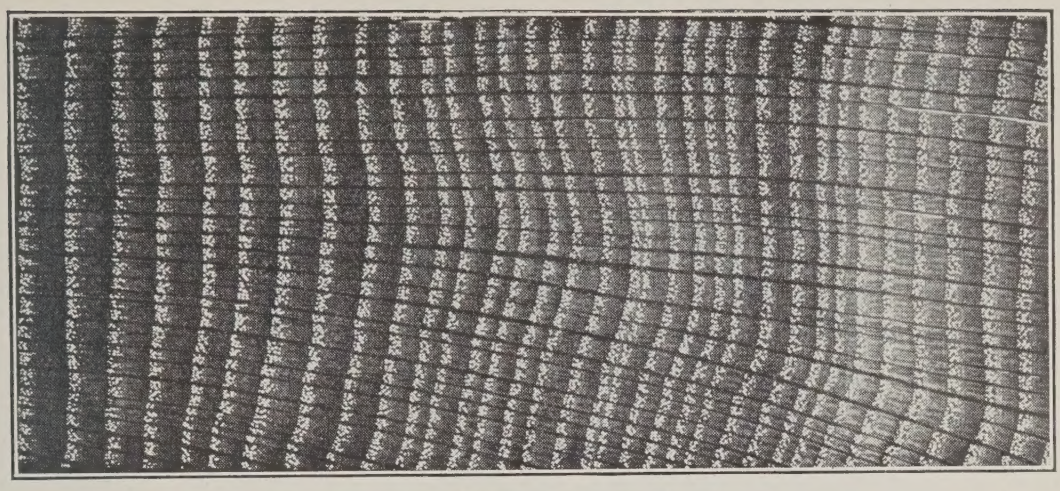


FIG. 161—Cross-section of wood of a mature tree of Red Oak (*Quercus rubra*), showing 32 layers of wood, intersected by the medullary rays which show black in the picture, which was taken by *transmitted* light (not by reflected light as is usual in photographing). The negative was made from one of the thin sections in Romeyn B. Hough's "American Woods." About 31 years of growth are indicated by the 32 layers. Why 31?

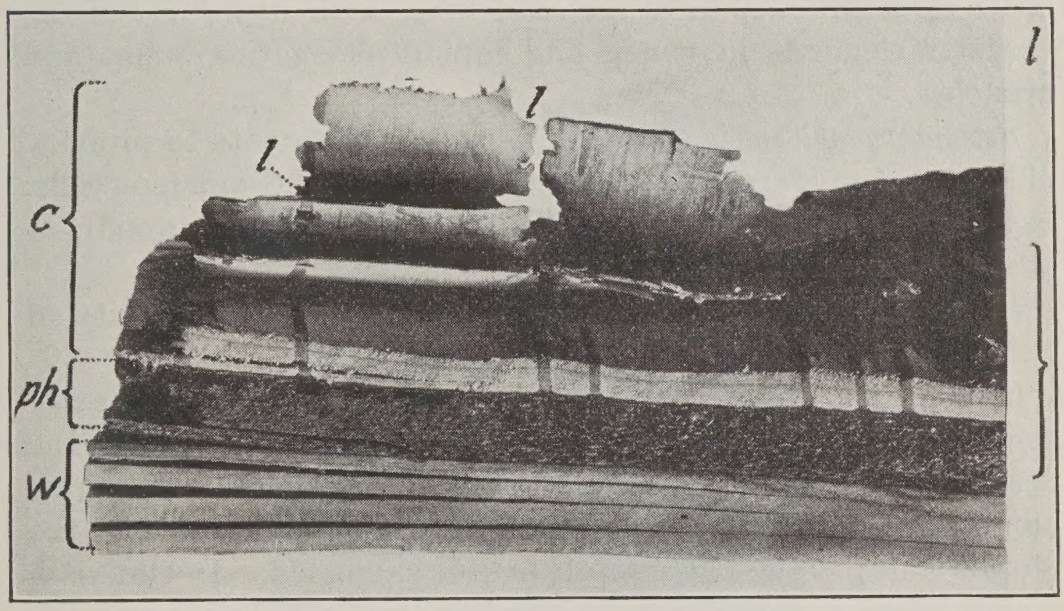


FIG. 162.—Piece of the fallen trunk of a canoe-birch (*Betula alba*). The annual layers of wood have become separated from each other by the early stages of decay of the wood. The two regions of the bark (periderm) are clearly shown; the inner (phelloderm), and the outer layer of cork that easily peels off in thin sheets. Between these two layers is the region of the cork-cambium that started by the cell-division of the hypodermal layer of the cortex in the young stem. The portion of the bark lying next to the wood is phloem and was derived from the cambium between the wood and bark, but the boundary between phloem and phelloderm, while evident in the specimen, does not clearly show in the half-tone, except at its lower end. The lenticels may be seen in face view and in section where they extend through the cork-layer.

may be laid down in a season. A prolonged drought, or the defoliation of a tree by some insect or fungous pest, followed by a new crop of leaves, may produce such a result. Thus it is evident that more than one layer of wood may be formed in a year, and hence the age of a tree may only be approximated by counting the "rings" of growth. When more than one layer is formed during a season each layer is commonly thinner than when only one layer is formed, and this makes it easier to read the history of the past in the histology of the wood.

In tropical countries, where there is no phenomenon of "change of seasons," as known in the temperate zones, but only rainy and dry seasons, the wood of dicotyledons occurs in layers, but they are not so closely correlated with the seasonal change as in the temperate zones.

Secondary wood comprises wood fibers, wood parenchyma, tracheids, tracheae, and bast fibers, but differs from primary wood in containing no vessels with annular or spiral thickening. This latter structure facilitates the stretching (without injury) of the vascular elements in young and rapidly elongating stems and branches.

Secondary phloem is similar in structural elements to primary phloem, comprising parenchyma, sieve-tubes and companion cells; bast fibers may be present, as in basswood (*i.e.*, bast-wood), or absent, as in alder, beech. birch, and others.

Secondary medullary rays are also formed by the activity of the cambium.

Secondary Cortex.—The epidermis and the primary cortex of herbaceous dicotyledons grows at practically the same rate as the tissues within, but in woody perennials the inner tissues grow more rapidly, and the primary cortex is finally obliterated by the tension and pressure to which it is thus subjected. In elm, oak, maple, birch, and other genera, the first layer of cells beneath the epidermis (*sub-epidermal* or *hypodermal layer*) resumes active cell-division, thus forming a cork-cambium, or *phellogen.*[1] The subsequent cell-divisions of the cork-cambium give rise to an outer layer and to an inner layer (*phelloderm*). These two layers,

[1] Phellogen, from the Greek φελλός (*phellos*), cork + γενής (genes), producing. It may arise in any region outside the cambium, but most commonly in the outer part of the cortex.

together with the phellogen and the secondary phloem produced by the cambium, are together known as the *periderm*, or *secondary cortex*.

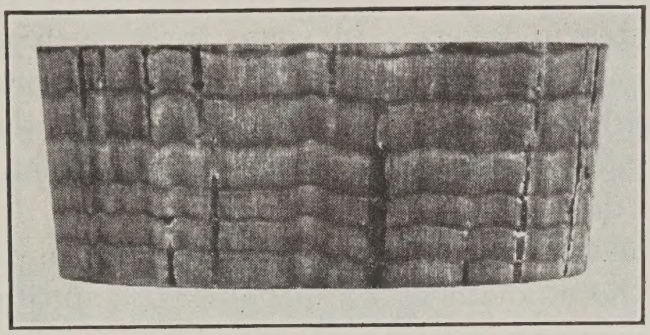


FIG. 163.—Reproduction of photograph of an ordinary bottle cork, showing annual layers of growth. How many years' growth is represented?

The cell-walls of the outer layer become *suberized* (impregnated with suberin), forming *cork*. Since no water can pass from the inner tissues out through the cork, the epidermis and other outer tissues in time become dry and peel off.

FIG. 164.—Portion of the trunk of a yellow birch tree (*Betula lutea*), showing the peeling of the outer and older layers of bark. (Photo by Roger Miller.)

The formation of periderm is not confined to the hypodermal layer. In some cases it develops from deeper lying cells, in other cases from the epidermis itself. The latter occurs in the cork-oak (*Quercus suber*), where the superficial periderm becomes

so thick as to furnish the *cork* of commerce, which often shows layers of annual growth (Fig. 163).

The characteristic peeling of the bark of birch trees (Figs. 162 and 164), is due to the formation of superficial periderm which easily separates in layers. In some trees, such as the plane trees (*Platanus*) and the pines, the phellogen produces cork-tissue in patches, causing the outer portion of the bark each year to fall off in large scales, often producing an undesirable litter around the trunk.

While the changes above described are going on, the phellogen underneath the stomata of the epidermis, bountifully supplied with air, develops an open tissue of thin walled cells. The rapid growth of this tissue causes the stomata to rupture in a manner characteristic for each species and giving a specific character to the bark. The ruptured stoma and the tissue underneath it constitute a *lenticel*, so named from its common lens-shape. The lenticles serve for the passage of air to the living tissues lying under the layer of cork (Figs. 95, 162, and 164).

Structure of Bark.—To summarize: the term bark (periderm) applies to all the tissues (taken together) outside the wood.

In *young stems* there are three distinct regions:

a. Inner bark or phloem, lying next to the wood. This is frequently composed largely of bast fibers, as in basswood bark. This region is often called *hard bast.* The phloem is also composed of parenchyma and sieve-tubes (with their companion cells) through which elaborated sap passes downward. This is the so-called *soft bast.* In some species bast fibers are wanting.

b. Outer Bark (Green Bark or Primary Cortex).—The cells contain chlorophyll and are the seat of photosynthesis (as in leaves). As the stem grows older the formation of the cork-layer in the outer part of the cortex keeps out the light so that the chlorophyll disappears and photosynthesis ceases. The primary cortex is finally obliterated by the growth and pressure of the tissues within.

c. Epidermis.—This disappears entirely in old woody stems.

In *old woody stems* there may be four tissues as follows, proceeding from the wood outward:

a. Phloem, produced by the cell-divisions of the cambium, and lying next to it.

b. Phelloderm, lying next to the phloem, and produced by the cell-divisions of the cork-cambium.

c. Cork-cambium (phellogen), composed of actively dividing cells, and lying between the layer of cork and the phelloderm.

d. Cork, outside the phelloderm, and also produced by the cork-cambium. This is impervious to air and is perforated by lenticels through which air may diffuse to the tissues underneath.

Buttresses and Braces.—Everyone is familiar with the buttress-like enlargement of many, if not most, trees just above

FIG. 165.—Base of the trunk of a Linden (*Tilia*), showing buttressing roots and also branches which have developed from adventitious buds on wound tissue.

the surface of the ground. (Fig. 165.) The formation of these buttresses, which are a natural feature of certain species, is favored by the fact that the constant swaying of the tree by the wind causes a back and forth bending at or near the ground. This keeps the bark loosened at that region and less resistance is offered to cambial activity and consequent growth in thickness there. Very often the buttresses are better developed on the down-hill side of trees standing on a slope, as the resistance to growth in thickness is less on that side than on the up-hill side. For similar reasons it is common for braces to develop on the underside of larger lateral limbs.

Origin of Branches. 1. *Stems.*—The branches of stems normally arise as buds which form in the angle between a leaf and the parent stem. This angle is called the *axil* of the leaf, and the bud an *axillary bud* (Fig. 166, a). The leaf is said to *subtend* the bud. Commonly only one bud occurs in the axil, but in the honey-locust (*Gleditschia*), honeysuckle (*Lonicera*), and several other species two or more buds may occur, one above the other (Fig. 166, b). In some species (*e.g.*, spice-bush—*Benzoin*) two or more buds occur side by side in the same axil (Fig. 166, e). Usually the bud is formed during the first season, rests over winter, and develops the second season into an *axillary branch.*

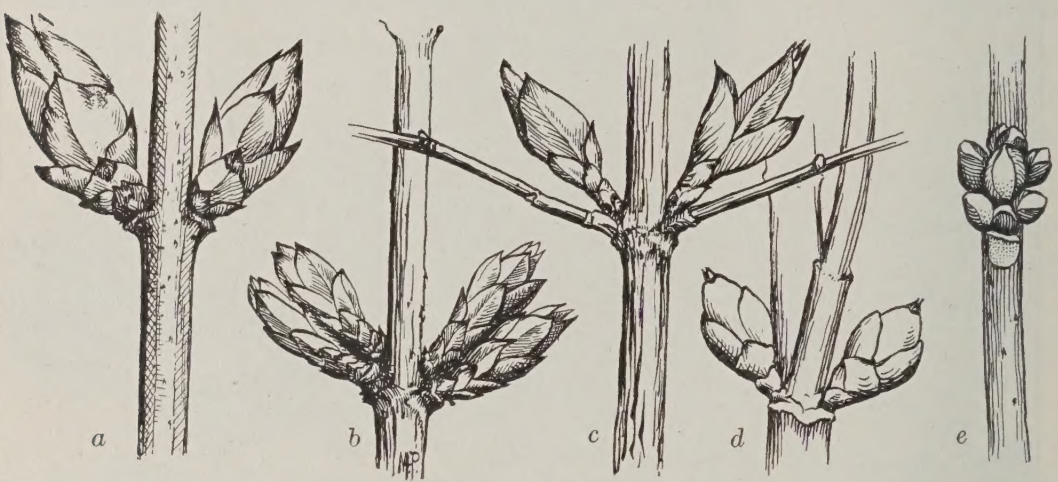


FIG. 166.—Axillary buds: *a*, Lilac (*Syringa*); *b*, honeysuckle (*Lonicera*); *c*, Late honeysuckle (variety of *Lonicera Maacki*); *d*, burning-bush (*Euonymus*) *e*, spice-bush, (*Benzoin*).

These buds first arise near the tip of very young stems from superficial embryonic tissue, lying just beneath the epidermis. They are thus exogenous in origin.

Stem buds may also arise in deeper lying tissues, and on roots or even on leaves, especially on wounds. Gardeners and horticulturists make use of this fact to propagate vegetatively by means of slips (*e.g.*, geranium), cuttings (*e.g.*, lilac), or even leaf-blades (*e.g.*, begonia). Such buds are called *adventitious.* One often sees branches or "suckers" growing from wound tissue where the scar of a sawed-off branch is healing over, or from the old wood near the base or buttresses of old trees (Fig. 165). Innumerable buds are sometimes found underneath the bark of mature trees. These adventitious buds may never come to

development as branches, but they are present to function when needed and constitute one of the "factors of safety" in plant organization (Fig. 167).

The advantage of adventitious or *supernumerary* buds is illustrated in such a case as that of the plane tree (*Platanus*), which sometimes loses all its leaves in early or mid summer as a result of the parasitic fungus (*Gleosporium nervisequum*). The lost leaves are commonly replaced by a second crop which develops on new branches which arise from adventitious buds.

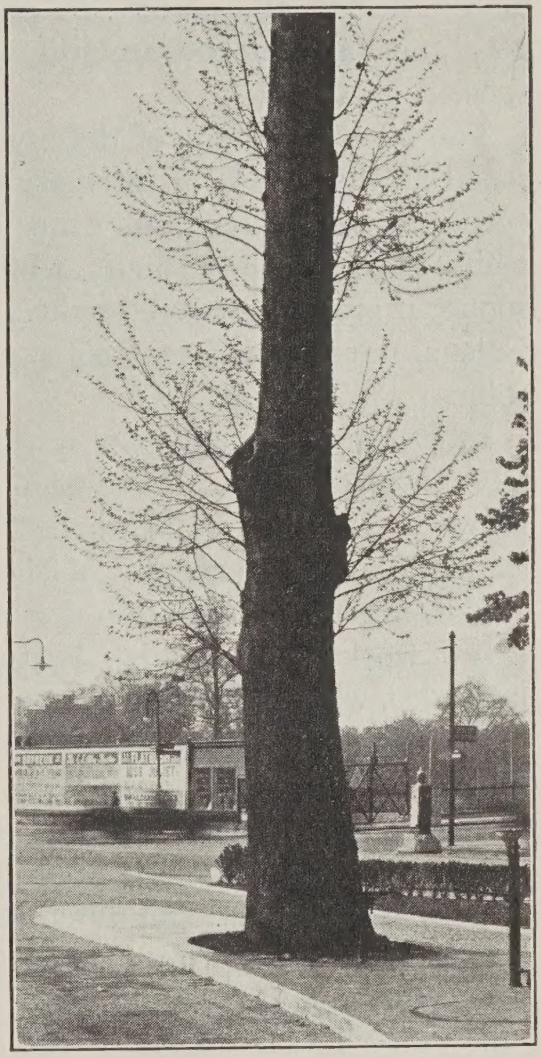


FIG. 167.—Trunk of a Sycamore (*Platanus*), showing small branches that have developed from adventitious buds located on wound tissue where large branches have been sawed off, and at other points on the trunk.

2. *Roots.*—In contrast to the origin of stem branches, the lateral branches of roots arise deep in the cortex, at the central cylinder of vascular tissue (Fig. 48). They make their way through the tissues of cortex and epidermis by mechanical pressure, and are commonly arranged in rows, lengthwise of the parent root.[1]

Effect of Light on Growth.—It has long been recognized that the effect of light on plants depends upon one or more of three factors: 1. Intensity, 2. Quality (that is, color or wave-length), 3. Duration of exposure. There appears to be a

[1] Following Van Tieghem (*Traité de botanique*, 2nd Edition, pp. 709–711. Paris, 1891), it was held for a long time that the passage of young lateral roots through the tissues of the cortex was facilitated by the dissolving of the latter by enzymes secreted by the endodermis. The work of Pond (*Bot. Gaz.* **46**: 410–421. 1908), clearly demonstrated the general absence of enzyme action, and that lateral roots emerge chiefly by mechanical pressure.

best intensity for healthy normal growth, and for many species this is less than the full direct light of the sun. In other words, many, if not all, plants do not need "all the light they can get," but only the best amount, which varies more or less with the species.

The effects of light of different color are not as well understood as the effects of intensity and duration. It is known that corn and beans and some other cultivated plants grow better in white than in colored light, while some plants come into flower sooner if grown under red light. Variegated leaves, like those of Coleus, develop different color patterns under light of different color.

In studying the effects of duration of illumination experimentally, three conditions have been tried. 1. Continuous illumination; 2. Continuous darkness; 3. Illumination for various fractional parts of each day of 24 hours.

Continuous illumination for 24 hours occurs in nature, for a few weeks only in high latitudes. Plants taken from lower latitudes, where they had been accustomed to the regular diurnal alternation of daylight and darkness, and transported to northern Norway were reported to have matured more rapidly and to have produced larger seeds. Plants grown in entire darkness usually fail to develop chlorophyll, and many species grow abnormally tall and spindling, and are also modified as to their internal anatomy. (See also pp. 283 and 284.)

Garner and Allard[1] studied experimentally the effects of differences in the length of the daylight period and found that the relative length of the day is one of the most important factors in the growth and development of plants. For each species there appears to be a most favorable length of day for growth, for tuber-formation, for flowering and fruiting, and for other activities. The shortening light period of late summer and fall favors tuber-formation in plants like potato. The shorter days of fall stimulate the flowering and fruiting of Chrysanthemums and other fall-flowering plants. Late bloomers, such as

[1] Garner, W. W. and H. A. Allard. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Res. **18**: 553–606. March 1, 1920. *Cf. ibid.* **27**: 119–156. Jan. 19, 1924.

Dahlias, may be forced to bloom during the summer by artifically reducing the length of their exposure to daylight. Poinsettia, which usually blooms only in the shortest days of winter (near Christmas) has been forced to blossom in August by reducing the daily light period to ten hours.

In other plants longer daily periods of light favor flowering. The radish, for example, forms its thick edible root (a vegetative activity) in the relatively short days of spring, and only comes into flower as the days grow longer. Red clover is another plant that requires relatively long periods of daily light in order to flower. It is well known that spinach cannot be grown in summer. The reason appears to be that the relatively long daylight periods of summer cause it to flower and "go to seed" instead of making the desired rosette of leaves for table use.

The "everflowering" and "everbearing" varieties of horticultural plants prove to be those kinds that are not sensitive to the relative length of daily light period.

On the basis of their experiments Garner and Allard state that, "The decreasing length of day of fall is an important factor in causing perennials to enter upon the winter period of dormancy. Abscission and leaf fall, also, appear to be induced by this shortening of the light period."

Photoperiodism.—The period of daylight most favorable for a plant is called by Garner and Allard its *photoperiod*, and the ability to respond to the change in relative length of daily period of light is *photoperiodism*. Plants that flower quickly in response to a suitable decrease in the light period are called *short-day plants;* those capable of coming into flower under the influence of a longer daily light period are *long-day plants*. No special term has been proposed for the third or intermediate group in which the greatest stem growth (vegetative activity) occurs with the alternation of light and dark periods of equal length such as occurs naturally within the tropics. In this group an increase of light period over darkness favors flowering, fruiting, and tuberization.

Knowledge of these facts should be of practical value to the farmer or gardener. A difference of only ten days in the date of planting, especially at a certain season of the year, might be sufficient to determine whether the plant would or would not

come into flower or produce edible leaves or tubers when desired. Much of this knowledge has already been worked out empirically, but an understanding of the principle of photoperiodism should make possible a more uniformly successful procedure, and at least save one from trying useless or foolish experiments.

CHAPTER XIV

ADJUSTMENT TO SURROUNDINGS

Environment.—Not only must plants be nourished and respire in order to live; they must also be in general harmony with their surroundings. The sum total of these surroundings is called the *environment.* Among the *factors of environment* are temperature, water, light, soil, gravity, air, electricity, ultraviolet rays, rays of radium, animals, and other plants. It will not be possible, here, to study the adjustments of the plant to all of these factors, but only to the more important ones, such as gravity, water, and light.

Stimulus and Response.—It is the nature of the various parts of a plant to grow in a certain definite relation to their environment. Thus, for example, main stems and roots normally grow parallel to the plumb-line, while their branches grow at an angle to it; foliage-leaves grow naturally in the light, while roots grow naturally in the dark. Any change in the environment requires a readjustment on the part of the plant, if the latter is to remain healthy. If the readjustment cannot be made, the given organ, or the entire plant, may become unhealthy, or may die. The change in the environment, considered from the standpoint of its effect on the plant, is called a *stimulus;* the readjustment or attempt at readjustment, a *response.* Thus, if a plant is growing at a certain rate at a certain temperature, any change in the temperature becomes a stimulus to which the plant responds by growing either more or less rapidly, as the case may be. The property of an organ by virtue of which it may detect any change in the environment is *irritability.* Organs and organisms are irritable because irritability is a fundamental property of all protoplasm. *Cf.* page 21.

Tropisms.—In addition to modifying the rate of growth when acting uniformly on all sides of an organ, any environmental factor may modify or determine the direction of growth by

acting on one side of an organ with more intensity than on any other side, or by acting predominatingly in one direction. The response to such a unilateral stimulus is a bending toward or away from the direction from which the stimulus comes, or transverse to its line of action. Such responses have been called *tropisms*—positive, negative, or transverse, each tropism being named from the nature of the inciting cause—for gravity, *geotropism;* for light, *phototropism;*[1] for water, *hydrotropism;* for contact, *thigmotropism;* for injury, *traumatropism;* for chemicals, *chemotropism;* and so on. However, since the organ is sensitive to the stimulus whether it can bend or not, it is an advantage to define tropism as that *kind of irritability by virtue of which an organ can detect the source or direction of action of a stimulus.* For mechanical or other reasons it may not be possible for the responding curvature to take place. It is not essential here to treat of all of the tropisms, nor of any of them fully, but a number of them, of special interest or importance in relation to crop plants, will be briefly discussed in the following paragraphs.

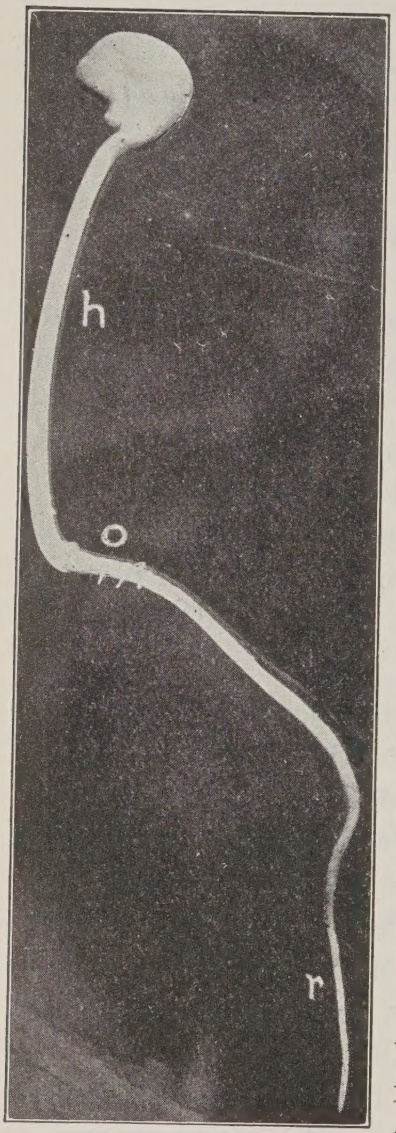


FIG. 168.—Seedling of white lupine (*Lupinus albus*), after having been placed horizontally in the dark for 48 hours. The hypocotyl (*h*) has responded negatively, and the root (*r*) positively to the stimulus of gravity. The portion (*o*) remains in the original horizontal position.

Relation of Roots and Stems to Gravity.—It is common knowledge that, in general, roots grow downward, while stems grow upward. If a germinating seed of lupine is so placed that the axis of the emerging embryo-plant is horizontal, the position of the elongating root and shoot after a given interval of time (*e.g.*, 48 hours) will be as

[1] Also called *heliotropism* (Greek, *helios*, sun + *tropos*, turning or bending). In pronouncing, the names of the various tropisms (except heliótropism) are properly accented on the second syllable.

shown in Fig. 168. The result is the same whether the plant is placed in diffused light or in the dark. The difference in the direction of growth may not, therefore, be attributed to the action of light. If the seedling is so placed that the only external unilateral influence is gravity—the attraction of the earth—the result

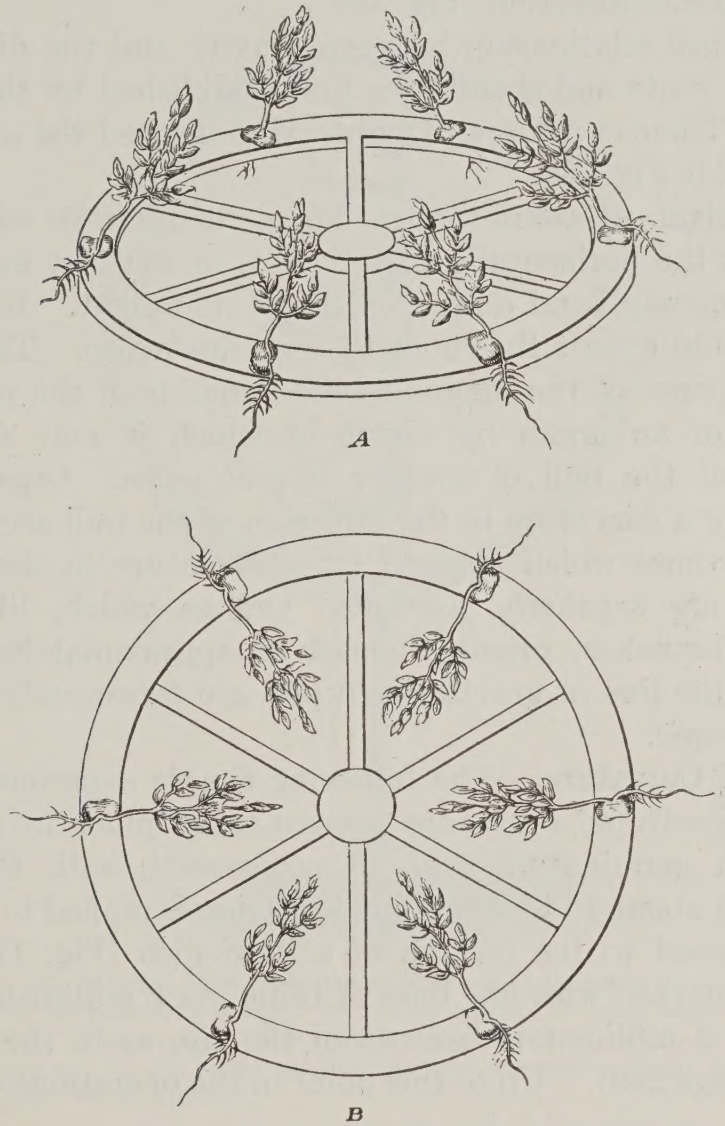


FIG. 169.—Knight's experiment, substituting centrifugal "force" for gravity. (After Knight.)

is as shown in the figure. We must, therefore, conclude that the result is due to the earth's gravitational attraction.

The correctness of this conclusion may be assured by subjecting the seedling to another influence than gravity, but, like it, acting on both root and shoot, at right angles to their long axes. Such

an influence is the centrifugal tendency produced by motion in a circle. If seedlings are fastened to a wheel, with the root and shoot pointing in various directions, and the wheel rapidly rotated, the growing root will bend until it points in the direction of the "pull" (centrifugal tendency), while the shoot will curve in the opposite direction (Fig. 169).

The causal relationship between gravity and the direction of growth of roots and shoots was first established by the English botanist, Thomas Andrew Knight,[1] who devised the experiment illustrated in Fig. 169.

Geotropism.—Careful thought about these results will make it clear that the horizontally placed root, in the first experiment, does not merely bend down because of its weight. If this were so, we would expect the shoot to bend down also. The curving is the response of the organs to the stimulus of the pull. The property of an organ by virtue of which it may detect the *direction* of the pull of gravity is *geotropism.* Organs which respond by a curvature in the direction of the pull are *positively geotropic*; those which respond by a curvature in the opposite direction are *negatively geotropic.* Organs which, like lateral roots or branches, orient themselves approximately at right angles to the line of gravitational pull are *transversely geotropic,* or *diageotropic.*

Zone of Curvature.—The following simple experiment shows that the geotropic curvature always takes place in a definite region. A germinating bean or other seed, with the sprout (*hypocotyl*) about 15 to 20 millimeters long, is pinned to a strip of cork, fastened to the bottom of a Petri dish (Fig. 170). The sprout is marked with fine lines of India ink 2 millimeters apart, beginning 2 millimeters back from the tip, as in the study of growth (page 249). Up to this point in the operations care must

[1] KNIGHT, THOMAS ANDREW. *b.* Herefordshire, England, Aug. 12, 1759; *d.* London, May 11, 1838. Noted horticulturist and plant physiologist, and first English plant breeder. He was one of the founders and the second president of the Horticultural Society (England), 1811–1838. His conception of gravity as the true cause of the vertical growth of the main axis of plants has been called (by J. Reynolds Green) "a flash almost of inspiration, one of those wonderful intuitions which are so rare, but which when they are realized start out new trains of thought and open the way to undreamed of results."

be exercised to keep the sprout as nearly parallel with the plumb-line as possible. By rotating the cork, or the entire Petri dish, the sprout is now fixed at right angles to the plumb-line, and the Petri dish covered and set in the dark.[1] The air in the dish may be kept moist by a strip of damp filter-paper placed around the circumference of the dish, inside. At the end of 12 hours, more

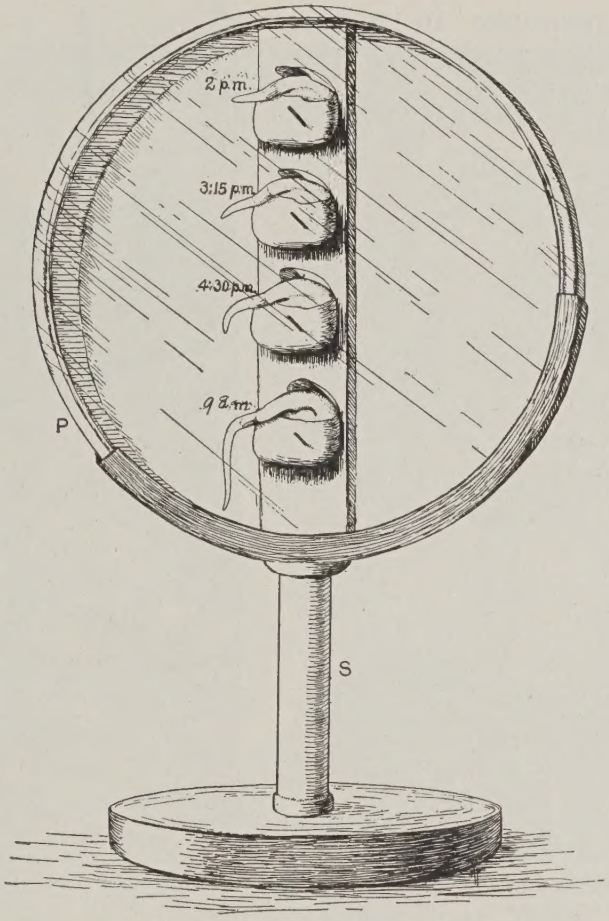


FIG. 170.—Experiment to demonstrate positive geotropism in the root of a seedling of lupine (*Lupinus albus*). *S*, metal stand; *P*, Petri dish, with edges lined with moist filter-paper. The seedling is pinned to a strip of sheet cork. The four views are of the same seedling at the successive hours as indicated. (Apparatus after W. T. Bovie.)

or less, the sprout, on account of its positive geotropism, will have responded to the pull of gravity by curving downward, until the portion between the curvature and the tip is parallel to the plumb-line. Examination of the ink-marks will show that *the zone of curvature is the same as the zone of maximum growth in length.*

[1] Why set in the dark?

The stimulus of gravity has modified the distribution of the rate of growth in such a way that the upper side of the sprout has grown more rapidly than the under side. After the sprout has become oriented in a vertical line, growth takes place by equal amounts, in equal periods of time, throughout the entire diameter, thus resulting in growth directly downward.[1]

Geotropic response in nature is illustrated in Figs. 171–173. Its value is evident in insuring good light-exposure and the efficient distribution of seeds and spores.

FIG. 171.—Negative geotropism in a barrigona palm (*Colpothrinax Wrightii*). By some accident, the palm, when younger, had been bent over.

FIG. 172.—Mullein (*Verbascum thapsus*) showing geotropic recovery of the terminal inflorescence, after having been bent over.

"Weeping" Trees.—The behavior of the branches of the "weeping" varieties of willow, beech, and various other species of trees would seem, at first thought, to be contrary to the

[1] Granting, of course, that all environmental conditions remain uniform on all sides.

principle that stems are negatively or transversely geotropic. This, however, is only an apparent exception, for the branches of such trees grow downward, not because they are positively geotropic, but because they lack sufficient mechanical tissue to hold them erect; they droop of their own weight.

Problems to Solve.—Many interesting questions now arise. How does the root, for example, "detect" the fact that its axis is

FIG. 173.—Negative geotropism in a fleshy fungus growing on a tree-trunk.

not parallel to the plumb-line? Have the root and the shoot a nervous system, or a brain? How is the bending accomplished? These questions should be given careful thought. They lead us into one of the most fascinating realms of plant study.

Effect of Light on Direction of Growth.—The fact that stems ordinarily grow toward, and roots away from the light, as mentioned above, is common knowledge. That this is the normal *response* of roots and stems to the *stimulus* of light may be shown

by a very simple experiment. A young seedling of mustard, or any other convenient plant is allowed to develop in complete darkness in ordinary tap-water, until its root and stem are each about 1 inch long. Being subjected to only the influence of gravity, the root grows vertically downward, the stem vertically upward. If the bottle and plant are then placed inside a covered box, to which the light is admitted only through a narrow slit in one side, the stimulus of the one-sided illumination will be

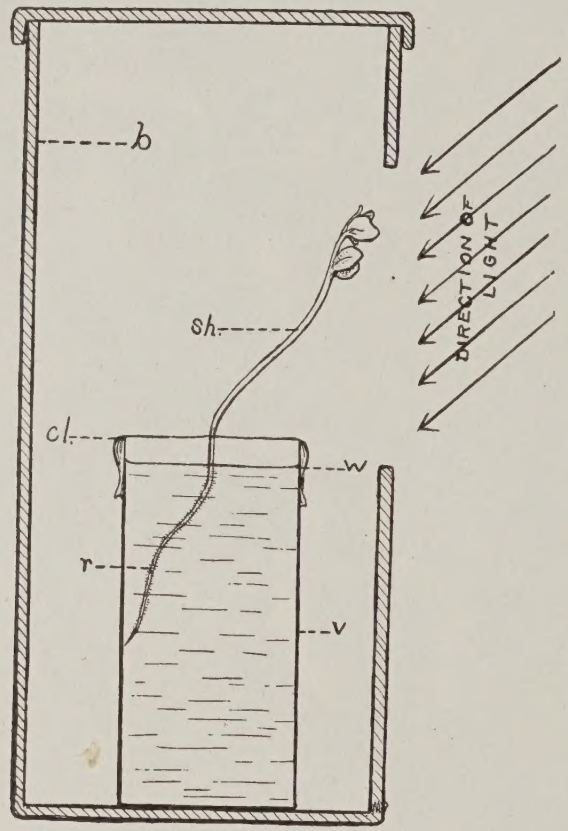


FIG. 174.—Phototropic response of a seedling of white mustard (*Brassica alba*). *b*, box, admitting light only through a narrow slit at the right; *v*, vial; *w*, water-surface; *cl*, cheese-cloth; *sh*, shoot; *r*, root.

followed by a curvature of the root away from the light, and of the stem toward the light, as shown in Fig. 174.

The result of the simultaneous stimulation of root and shoot by light and gravity is illustrated in Fig. 175.

Phototropism.—The property of an organ by virtue of which it may detect the *direction of the source* of incident light rays is *phototropism.* Organs which respond by a curvature in the direction of the source of light are *positively phototropic;* those

which respond by a curvature in the opposite direction are *negatively phototropic*. Like geotropism, phototropism is a special kind of irritability. Organs growing in the light are, of course, subject to the influence of both light and gravity at the same time.

Phototropic response in nature, is shown in Figs. 176 and 177.

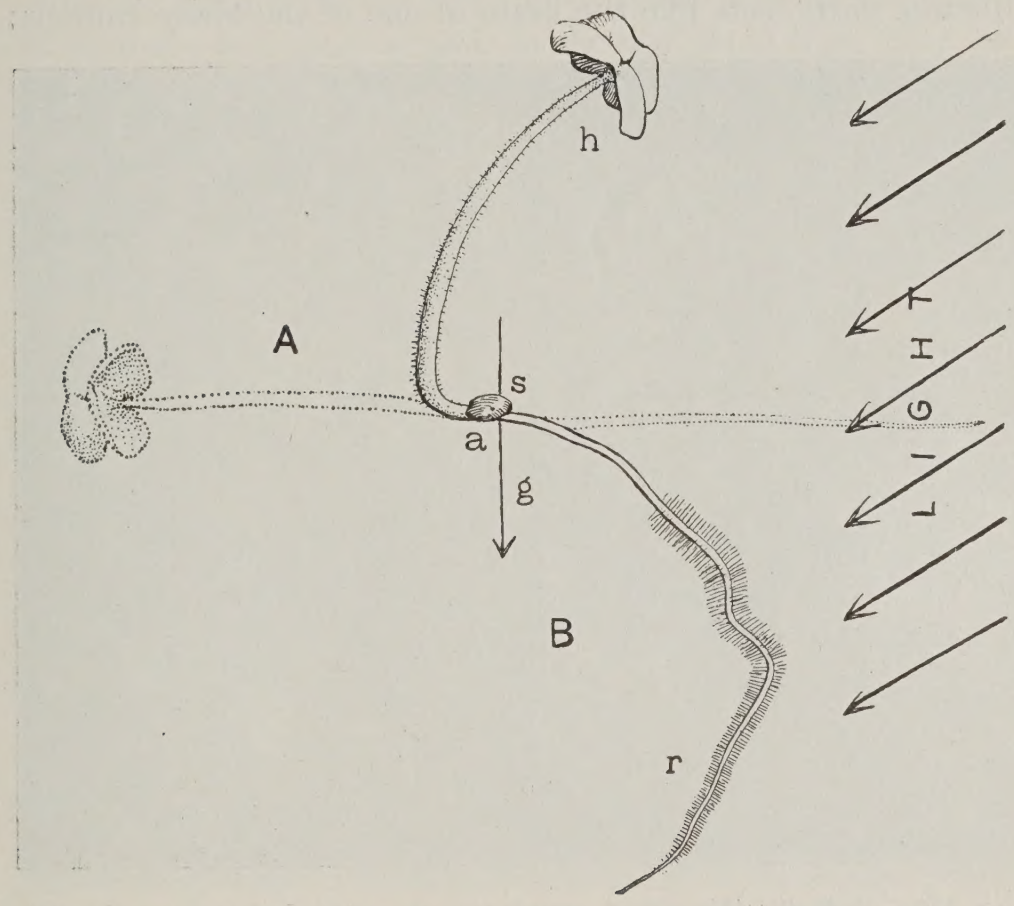


FIG. 175.—Seedling of white mustard (*Brassica alba*) showing the combined effect of light and gravity on the direction of growth of root and shoot. The dotted line figure indicates the position of root and shoot at the beginning of the experiment. The change indicated was accomplished in about 48 hours. (Cf. Fig. 170.)

Function of the Root-tip in Tropisms.—Careful experiments of Charles Darwin and others have demonstrated that in geotropism, phototropism, traumatropism (sensitiveness to injury), and thigmotropism (sensitiveness to contact), the sensitive region is confined to the root-tip—the region between the root-cap and the zone of elongation. The stimulus is "perceived" by the cells of the root-tip and transmitted thence to the zone of growth where the response takes place. When the root-tip is carefully

cut off the root no longer responds by bending when exposed to the one-sided influence of gravity, light, injury, or contact.

"We believe that there is no structure in plants more wonderful as far as its functions are concerned, than the tip of the radicle . . . It is hardly an exaggeration to say that the tip of the radicle, having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals;

FIG. 176.—Daffodils (*Narcissus*) growing on the south-facing slope of a hill. Note that the flowers all turn (nutate) in a general southerly direction, toward the brightest light.

the brain being seated within the anterior end of the body, receiving impressions from the sense organs, and directing the several movements."[1]

But while, in the above tropisms, sensitivity appears to be confined to the root-tip, studies of Hooker[2] with *Lupinus albus*,

[1] Darwin, Charles. The power of movement in plants. p. 576. New York, 1900.

[2] Hooker, Henry D. Hydrotropism in roots of *Lupinus albus*. Ann. Bot. **39**: 265–283. April, 1915.

and earlier studies of other investigators show that hydrotropic sensitivity is not confined to the root-tip (at least in *Lupinus*), but also resides in the short region of growth, just above the tip.

Do Plants Have Nerves?—We raised this question on page 277, In the early days of plant anatomy investigators were impressed with the resemblance of the fibro-vascular strands to the nerves of animals, and these strands in the leaf-blade were often called

FIG. 177.—Hay-scented Fern (*Dicksonia punctilobula*) growing in the edge of a wood. Note that the fronds all face away from the shade of the wood toward the sunlight. (Photo by E. L. Crandall. Courtesy, Wild Flower Preservation Society, Washington, D. C.)

"nerves" as well as veins. In 1914 Ricca found that a stimulus can be transmitted through a strip of wood of one of the sensitive plants (*Mimosa*) from which all fibro-vascular tissue has been removed for a considerable distance. The stimulus travels through the wood, even when it contains no living cells. Evidently the transmission of the stimulus in plants is not a vital process like the nerve stimulus in animals. Ricca showed further that the stimulus is carried by the transpiration current in the

form of a *hormone*. Hormones, so named by the physiologist Starling, are substances secreted by a tissue or organ from which they are transmitted (by the blood or lymphatics in animals, by the transpiration current in plants) to another organ where they produce their effect.[1] For example, the entrance of food into the duodenum of the human intestine causes it to secrete a hormone which is carried to the pancreas which is thereby stimulated to secrete trypsin. The trypsin, in turn, passes to the duodenum and continues the digestion of the food whose presence there caused the secretion of the hormone.

So in plants, Ricca showed that the stimulated region secretes a hormone which travels to the region of response and causes the reaction to the stimulus. It has been further found, by the combined experiments of a number of plant physiologists, that when, for example, the tip of a seedling of wheat or oats is subjected to illumination on one side only, the "stimulus" will pass down to the zone of growth and cause the seedling to bend toward the light even after the tip has been cut off and replaced. The "stimulus" will even pass through a slice of pith 0.1 mm. thick, soaked in gelatine and placed between the cut surfaces of the stem and the severed tip. Boysen-Jensen went a step farther and showed that the tip of one plant may be transferred to the decapitated stem of another plant, and the "stimulus" will be transmitted to the responsive region of the latter causing it to bend.

The stimuli of gravity, contact, and injury are transmitted in a similar way. These experiments all indicate that the stimuli are transmitted by means of hormones, carried in the transpiration stream from the stimulated region to the region of response, and the studies of Dixon and others indicate that the hormones are carried through the wood of the vascular bundles.

Effect of Light on Rate of Growth.—Everyone is familiar with the fact that stems grown in darkness, or in reduced light, are commonly much elongated, and bleached to a pale yellow color, or even to white. The chlorophyll has failed to develop. This condition is called *etiolation*. Early studies of this phenomenon seemed to indicate that light retarded growth in length, but more

[1] The term *hormone* is from the Greek verb *hormao* (ὁρμάω), which means to stir up, to *start*, or to *incite*, hence to *stimulate*.

FIG. 178.—Seedlings of the white lupine (*Lupinus albus*). At the left, grown under normal illumination; at the right, grown in darkness. Both cultures are of the same age.

FIG. 179.—*Calla palustris*. *A*, Normal plant, grown in daylight; *B*, etiolated plant of the same age, grown in darkness. (After D. T. MacDougal.)

thorough and more extended observations clearly showed that such is not always the case. The stems of many kinds of plants (*e.g.*, potato, pea, bean) undoubtedly grow much longer in darkness than in light (Fig. 178), but in other species the difference, if any, is much less (Fig. 179). A disturbance of the normal illumination causes a general disturbance of the functions of the organ or of the entire plant, so that not only growth, but differentiation of tissues (development), nutrition, and metabolism in general are more or less upset, and proceed in an abnormal manner.[1] Under conditions of normal illumination (granted, of course, that all other conditions are normal), the physiological processes of the plant are *regulated* in a normal manner; but when the illumination is abnormal, healthy regulation ceases, and the organ behaves abnormally. This abnormal behavior includes the failure of chlorophyll to develop, and irregularities of growth. With many plants the stems grow abnormally long and slender, suggesting that absence of light favors more rapid growth in length.

Relation of Leaves to Light.—More than all other organs of the plant, the foliage-leaf is developed and adjusted with reference to illumination. Its form, dimensions, and internal structure, and its attitude and position on the stem are chiefly expressions of the surrounding conditions of light, and clearly indicate that the chief function of leaves is to bring the plant into suitable relation to light. Its flat, expanded form makes possible the favorable exposure to light of a large amount of chlorophyll, upon which the plant is absolutely dependent for the manufacture of its food. Leaves that develop in reduced light-intensity (shade), ordinarily dispose of their tissue in such a way as to become thinner and of larger area than when developed in more intense light. When the light-intensity is increased, the palisade layer often becomes double (Fig. 40). If a leafy stem is bent, so as to bring the leaf-blade into poor light-exposure, the leaf-stalk, in some plants, will bend and twist so as to restore the blade to a suitable light-relation.

[1] It is often stated in "popular" writings that stems grown in darkness "reach for" or "seek" the light. A careful consideration by the student of all that these terms imply, when predicated of a plant, will lead at once to a recognition of their incorrectness, and even of their absurdity.

The leaves of some plants (*e.g.*, nasturtium) remain adjustable to the direction of incident light during their active life (Fig. 180); the leaflets of legumes and some other plants (Fig. 181) fold together each night and on cloudy days, thus manifesting the so-called "sleep" of plants. Whether this response is of value to the plant is not entirely certain. In other plants (*e.g.*, the house geranium) the leaves have a *fixed light-position*, and after reaching maturity are not able to readjust themselves to changed conditions of illumination (Figs. 182 and 183).

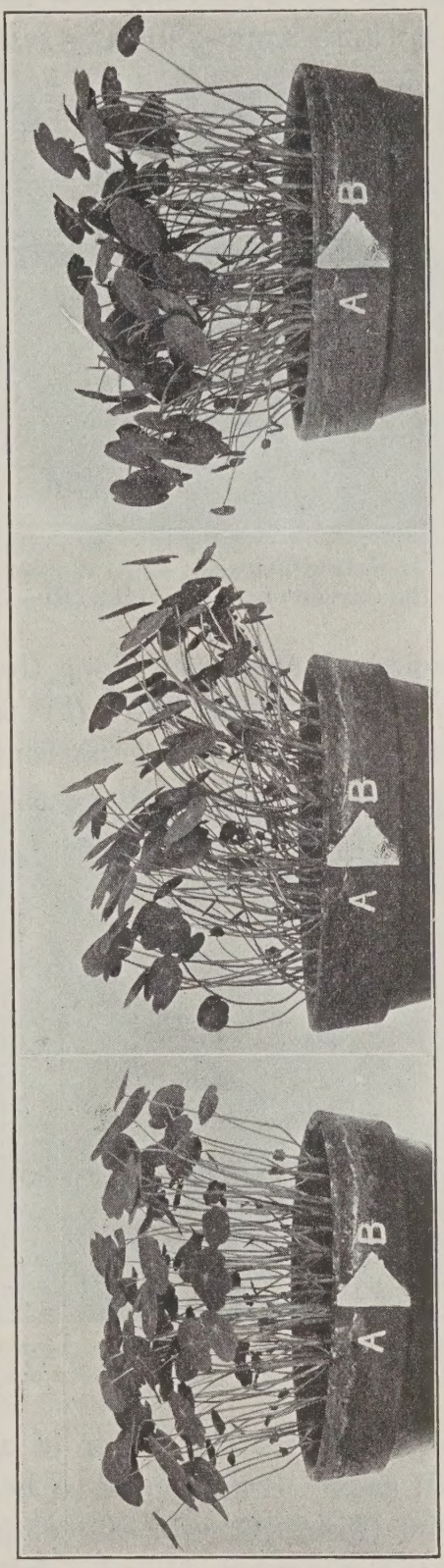


FIG. 180.—Experiment to illustrate adjustable light position. Seedlings of nasturtium (*Tropaeolum majus*). At left, at beginning, seedlings grown under equilateral illumination; in middle, after 48 hours of illumination from the right side only; at right, same culture as in the middle, after receiving illumination for 48 hours from the left side only.

Hydrotropism.—The ability to detect and respond to the direction of most favorable conditions of moisture is chiefly illustrated by roots. This is shown by a simple experiment. A glass bottomed dish is filled with fairly dry soil, and seeds of any convenient plant are sown in a row across the dish near the middle. The soil is then watered *at one side only* at a point 90° from the ends of the row. By capillarity the water spreads through the soil toward the seeds. The amount of water must be carefully adjusted to insure enough for the germination of

the seeds and, at the same time, keep the soil on the opposite side of the seed-row too dry to favor root-growth. The dish must be kept approximately horizontal. As the roots develop

FIG. 181.—Potted plants of an oxalis showing the position of the leaflets during the day (*A*) and the night (*B*)—the so-called "sleep" of plants.

they will turn and grow along the bottom of the dish, chiefly in the direction of the most favorable water supply (Fig. 184). Hydrotropism results in the roots of willows growing in large

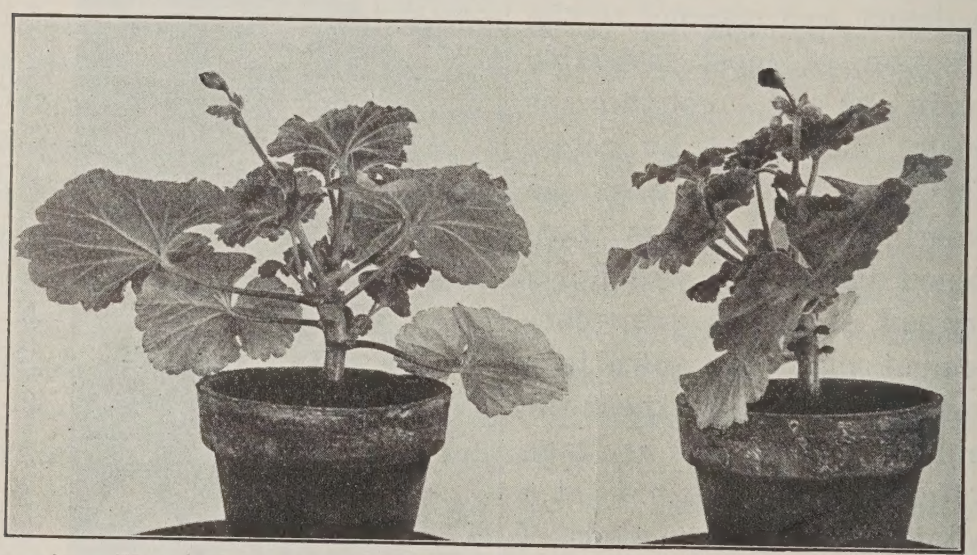


FIG. 182.—House geranium (*Pelargonium*), showing back and side views of the same plant, grown with the same side always facing a window. (Cf. Fig. 183.)

numbers out into the water of a nearby stream. It also frequently causes drain pipes to become choked by the roots of adjacent trees. One of the chief offenders in this respect is the Carolina poplar (*Populus deltoides* Marshall), often planted

as a shade tree in city streets. In the city of Newark, New Jersey (U. S. A.) the clogging of street drains by the roots of this tree

FIG. 183.—House geranium (*Pelargonium*). At the left, front view of the same plant as shown in Fig. 182. At the right, about three days after having been reversed, in front of the window. Note that only the upper, younger leaves are properly adjusted to receive the light rays on their upper surfaces; the lower, older leaves were not able to change the "fixed" light position they previously assumed.

became such a nuisance that the Department of Sewers and Drainage requested the Shade Tree Commission to refrain from

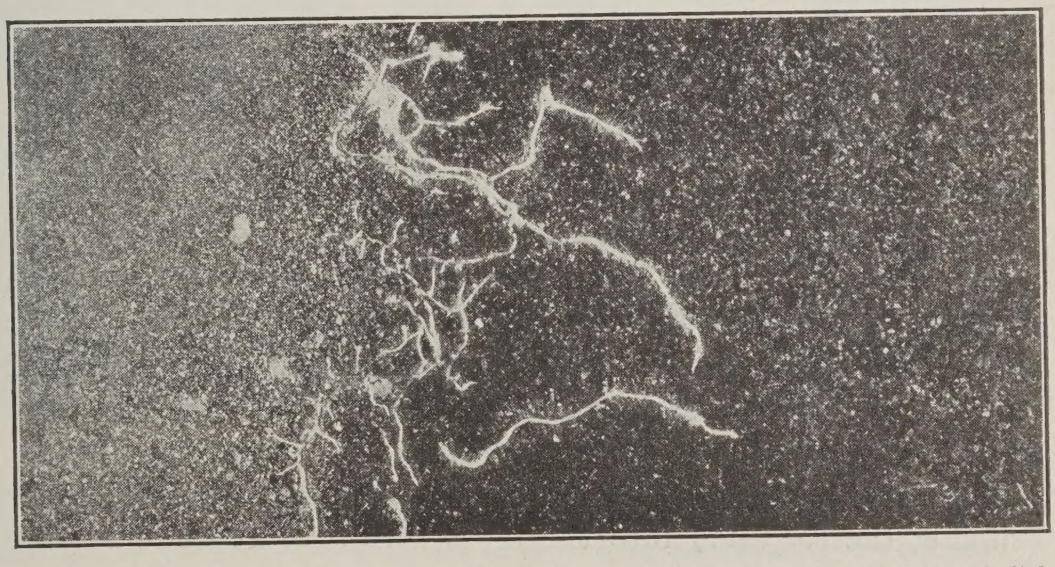


FIG. 184.—Roots of white mustard seedlings growing in a glass bottomed dish and watered only from one side (the right). Note that the roots all grow toward the moister soil, illustrating hydrotropism.

further planting of this species. It was found that the roots worked their way through the joints of tile pipe even when they were carefully cemented. After entering, the roots branch pro-

fusely and practically fill the pipe. Roots of willow, elm, and grass also cause similar trouble. Stone[1] has reported the case of a 12-inch tile drain pipe being badly clogged by the roots of a single off-shoot of a pear tree growing about seven feet away. Only one root entered the tile, being somewhat flattened where it passed through, and having a diameter of about five-eights of an inch inside the tile. It then subdivided, again and again. A count of the annual rings of growth showed that the root had required only five years to clog the drain. The *mass* of roots measured 61 feet in length, but the length of the individual roots was 8498 feet, or over one and six-tenths miles. Stone estimated that if the length of all the smaller rootlets, ranging from a few to several inches in length, were added, the total length of the root-system would exceed two miles. This, of course, is greater than the length of the root system of a pear tree growing normally in soil.

Carpotropism.—Interesting tropistic movements are commonly manifested by the peduncles or flower-stalks of many plants. In some plants the underside of the stalk grows most rapidly (hyponasty) up to the time when the bud is formed, giving the bud an upright position; then, when the bud begins to open, the stalk resumes its growth but the upper side grows most rapidly (epinasty), causing the flower to bend down (Figs. 185–186). The position may be again reversed after pollination or as the fruit begins to form. In other plants the buds are pendent, then the flower-stalk bends up as the flower opens, and finally down again, after pollination, when the fruit and seed are forming. Different sequences of position are characteristic of different species. In many cases the change of position of the flower stalk seems to be advantageous, either placing the bud and flower in such a position as to afford protection to the pollen against rain, or facilitating cross-pollination by insuring insect visits, or bringing the seed-pod into the most favorable attitude for the dissemination of the seeds. In other cases it seems difficult to see what, if any, advantage is secured. (See also p. 358.)

Correlation within the Plant.—It is of interest to note that the parts of a plant are not only sensitive to the stimulus of their

[1] Stone, G. E. The clogging of drain tile by roots. Torreya **11**: 51–55. 1911.

surroundings, but are correlated, or adjusted to each other in this respect. This correlation modifies their reaction to external stimulation. Thus, if the "leader," or main stem, of a tree is

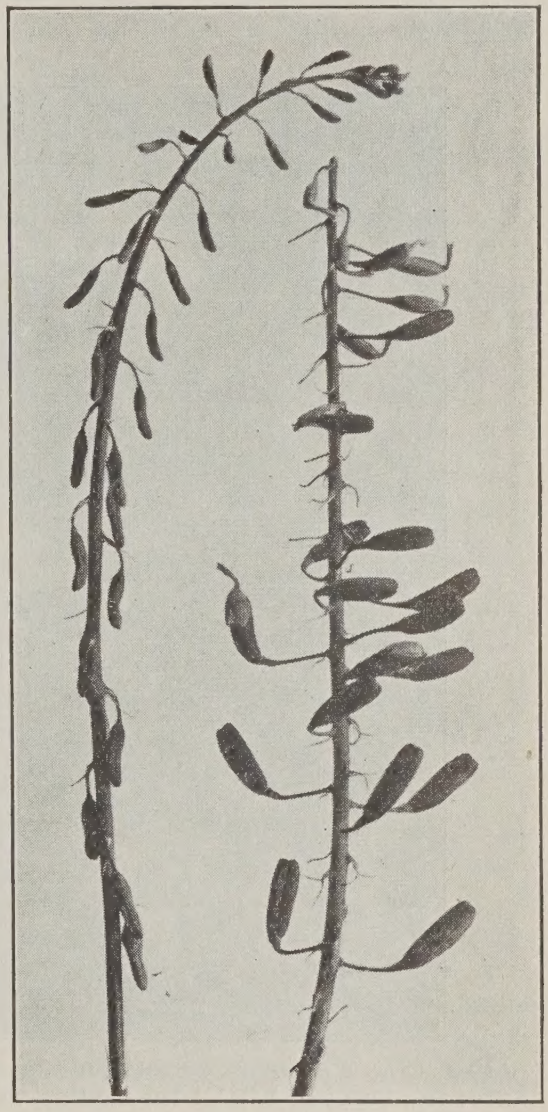


FIG. 185. FIG. 186.

FIG. 185.—Inflorescence of the Summer Hyacinth (*Galtonia*), showing carpotropism. The flower buds are erect at first, drooping after anthesis, and after pollination the peduncle bends upward so as to bring the (ripening) ovary into the erect position again. The movement, both downward and upward, is through an arc of 180° (Cf. Fig. 186).

FIG. 186.—Two flower-stalks of a species of *Gasteria* (a tender plant of the Lily Family), showing carpotropism. The flower-buds are upright, the open flowers pendent. At the right the ripening seed-pods are seen in various stages of resuming the upright position. This flower-stalk may at first have bent over to the left by the weight of the seed-pods and they had not all become readjusted to gravity after the stalk was straightened up prior to taking the photograph. (Cf. Fig. 185.)

destroyed, one or more of the lateral branches will turn upward, in what appears to be an "endeavor" to perform the functions of a leader (Fig. 187). In other words, the destruction of the leader alters the mode of reaction of the lateral branches to the pull of gravity.

FIG. 187.—Geotropic correlation among the branches of a young spruce tree. After the terminal bud of the sapling was destroyed one of the lateral branches (normally transversely geotropic) became negatively geotropic; ultimately it assumed a vertical position and became the "leader" of the tree.

Correlation among Leaves.—On a vertical and equally illuminated branch, as of maple, the petioles of the lower leaves are longer than those above them, and the stalks of opposite leaves are usually about equal in length (Figs. 188 and 189). But on horizontally growing branches, the attitude of the leaves is profoundly altered. The length of the petioles, and their attitude is such as to insure the placing of the blades in positions for the most

favorable illumination. This often results in a marked twisting and bending of the leaf-stalks. Blades of opposite leaves often do not appear to be opposite each other, and are often of very unlike size. Such an arrangement of the blades forms a *leaf-mosaic* (Figs. 190 and 191). If a leaf is removed from a group, or even if a leaflet is removed from the blade of a compound leaf, the remaining leaves or leaflets will alter their positions with reference to each other so as to occupy the space most advantageously and economically (Fig. 192).

FIG. 188.—Vertically growing branch of a maple, side view, showing elongation of the petioles of the lower leaves, which serves to prevent their being shaded too much by the leaf-blades above them. (Cf. Fig. 189.)

Advantages of Power of Adjustment.—Very little thought will enable one to understand at once the profound significance to the plant of its ability so to adjust its organs as to bring them into harmony with surrounding influences. If a stem, bent over, could not erect itself, if leaves could not assume positions that secure the most favorable illumination, if stems and leaves were not correlated with each other, most plants would soon be out of harmony with their environment and would sicken and die. Fully one-half the leaves of the Motherwort, illustrated in Fig.

193, would have been deprived, by adjacent plants, of suitable illumination, had they not possessed this power of adjustment.

Importance of Tropisms in Agriculture. *a. Geotropism.*—The response of plants to gravity, like the flow of rivers or the heat of the sun, is one of the numerous things we have always been so familiar with that it seldom, if ever, occurs to most men to ask the cause. It is taken for granted because it has always been so. Treatises on botany continued to be published for eighteen hun-

FIG. 189.—Adjustment of leaves, by the lengthening of the petioles, to secure the best illumination, in maple. Top view of same branch as in Fig. 188.

dred years (from Aristotle to Darwin) without such a question as this being raised—much less investigated. It is difficult for us to understand this lack of inquisitiveness or curiosity (not to mention scientific interest) as to the cause of a process which really makes agriculture possible, since it lessens the work and worry of the farmer to a degree that can hardly be over-stated. To appreciate this, one has only to imagine what it would mean to the farmer if plants were not sensitive to gravity and did not

respond to this stimulus just as they do. In such an event every seed planted, for example, would have to be placed in the ground right side up, with the greatest care to have the root portion pointing downward and the stem portion upward—in other words, to have the main axis of the plant in a vertical line. Were this the case, such a process as the sowing of seed broadcast would, of course, be quite out of the question. (*Cf.*, p. 754, Footnote 3.)

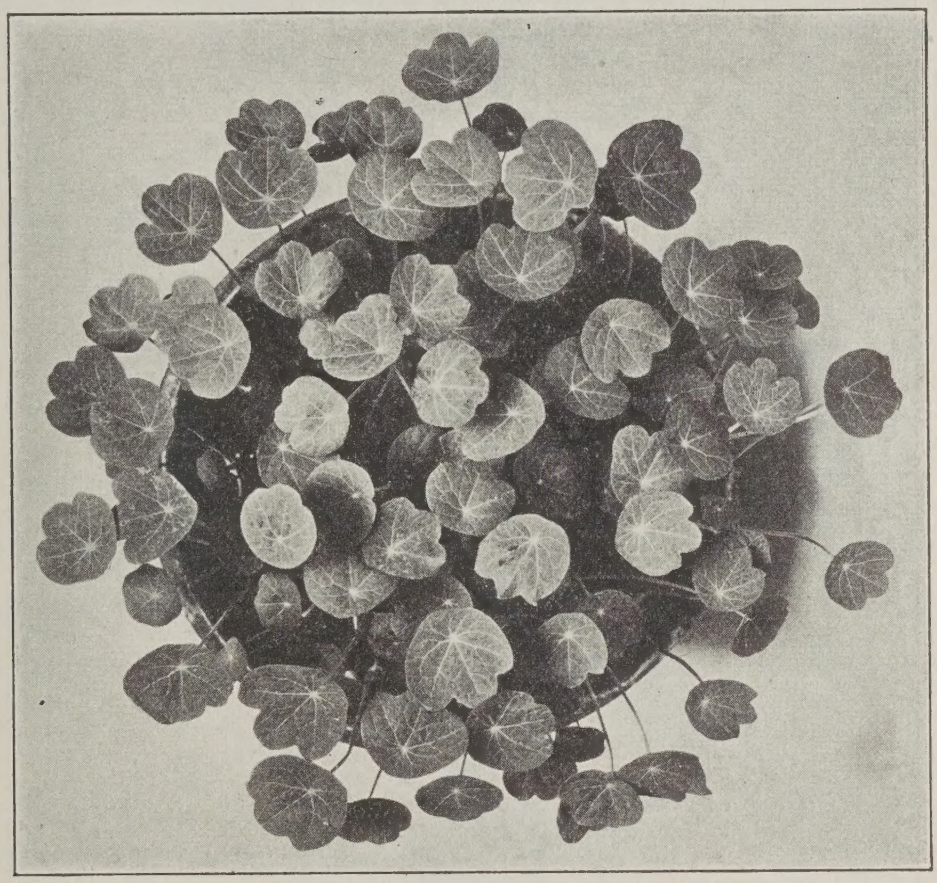


FIG. 190.—Garden nasturtium (*Tropaeolum majus*), showing leaf-mosaic in seedlings. Top view; compare Fig. 180, showing other views of the same seedlings.

Painstaking experiments have proven that the geotropic sensitiveness of the root resides in the root-tip.[1] The most extensive study of this question was made by Charles Darwin,[2]

[1] The crucial experiment was reported in 1894 by Pfeffer in a paper before the British Association for the Advancement of Science (*Annals of Botany* **8**: 317–320. 1894).

[2] The Power of Movement in Plants. Chapters XI and XII, New York, 1900.

and his classical description of the course of the growing root through the soil in response to the stimulus of gravity gives a vivid picture of the process and of its great importance to the plant. We may feel almost sure, says Darwin, "that when the

FIG. 191.—Plant of *Begonia metallica* showing leaf-mosaic. The blades are all adjusted to each other in position so as to secure the most favorable illumination possible. (*Cf.*, Fig. 395.)

tip encounters a stone or other obstacle in the ground, or even earth more compact on one side than on the other, the root will bend away as much as it can from the obstacle or the more resisting earth, and will thus follow with unerring skill a line of least resistance . . . We believe that there is no structure in

plants more wonderful than the radicle . . . The course pursued by the radicle in penetrating the ground must be determined by the tip; hence it has acquired such diverse kinds of sensitiveness. It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals."

It is a common experience on the farm to have a field of grain laid nearly flat by a severe wind storm. If the crop is not too near maturity the plants may recover, sufficiently to avoid entire

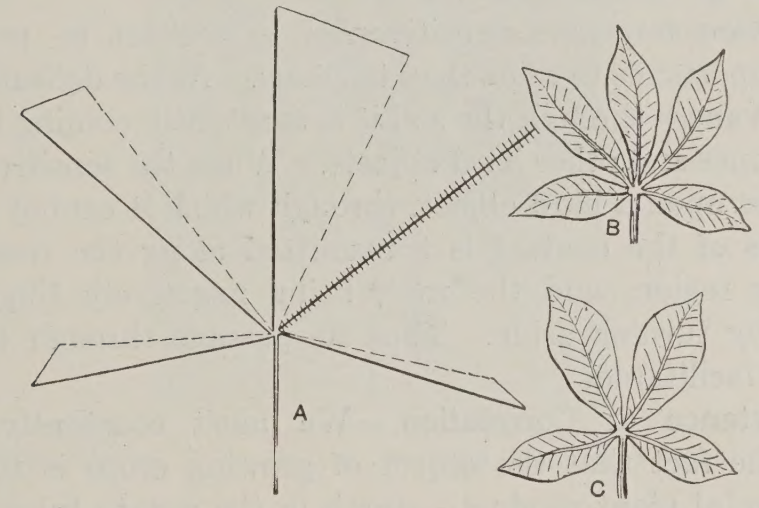


FIG. 192.—Effect of removal of a leaflet from a palmately compound leaf (*e.g.* Woodbine). *B*, normal leaf; *C*, after removal of upper right-hand leaflet. *A*, Unbroken lines represent average normal position of leaflets; dotted lines, average position of leaflets after operation; barred line, position of leaflet removed. (*A*, after Zeleny.)

loss and make harvesting possible, by the geotropic response through which the plants again become erect.

In the case of trailing vines, such as squash, cucumbers, and other cucurbits, the negative geotropism of the tip of the stem helps to prevent its being injured by rubbing against the ground as the stem grows in length.

b. Phototropism.—Recalling that the food of plants is made chiefly in the leaves, and that the energy is that of sunlight, we can at once appreciate the necessity of having the leaves so organized that they may detect the direction of the source of light and orient themselves in such a way as to secure the most favorable illumination. The leaves of horizontal stems, for

example, may, under the stimulus of light, twist and turn on their leaf-stalks in such a way as to bring the flat surface of the leaf-blade into a position that will insure the best possible illumination. Were this not possible, the leaves of such trailing stems as melons and pumpkins would present the edges of their leaf-blades to the sun, and would not then receive sufficient energy for the work of photosynthesis.

c. Hydrotropism.—This property of roots is of agricultural advantage chiefly in condition of drought, and in artificial irrigation, where water may be unequally distributed in the soil and in deficient quantity.

d. Thigmotropism.—Sensitiveness to contact is, perhaps, of more importance to roots than to stems. As the delicate growing root advances through the soil it is constantly coming in contact with stones and other hard objects. When the sensitive root-tip impinges upon a hard object, through which it cannot grow, the stimulus of the contact is transmitted along the tissue to the growing region, and the root, being negatively thigmotropic, reacts by turning aside. Thus its passage through the soil is greatly facilitated.

Importance of Correlation.—We must constantly keep in mind the fact that the object of growing crops is to produce some useful plant product—starch in the potato tuber, banana, and corn grain; sugar in the cane and sugar beet; fiber in Manila hemp and flax; latex in the rubber tree, etc. The production of such substances in commercially profitable quantities is a function of photosynthesis, which takes place chiefly in the leaves. Hence, the ability of leaves to adjust themselves to others on the same or adjacent plants is of prime importance. Were the formation of leaf-mosaics not possible, the yield of many crops would be greatly reduced.

As a result of internal correlation lateral roots grow roughly horizontally, being transversely geotropic, so long as the main root remains positively geotropic. As a direct result of this adjustment the plant is not only more firmly anchored in the soil, but the roots may explore a much larger territory, thus insuring with more certainty an adequate water and food supply (See pp. 33–40). If the tip of the main root is injured or

destroyed, as may often occur in nature, one of the secondary roots will assume the leadership and grow vertically downwards,

FIG. 193.—Motherwort (*Leonurus Cardiaca*), showing adjustment of leaves to light. This plant grew at the edge of shrubbery, receiving relatively little light from behind.

similar to the behavior of branches under similar circumstances (p. 290).

PART III
REPRODUCTION AND LIFE HISTORIES

CHAPTER XV

REPRODUCTION

All of the structures and processes discussed in the preceding chapters have had to do primarily with maintaining the life of the individual, and yet, as everyone knows, individuals do not live forever. This is as true of plants as of animals, though the former may live much longer than the latter. The oldest animal of which there is any authentic record is the Aldabra tortoise, known to be over 160 years old,[1] but many trees live to be several hundred years old. A white Oak in Flushing, N. Y. lived to be over 660 years old. Some of the giant redwoods (*Sequoia gigantea*) of California are known to be at least four thousand years old. Until recently the giant redwoods were supposed to be the oldest living things, but it has now been ascertained that the Big Tree of Tule, 250 miles southeast of the City of Mexico, is at least 5000 years old. This tree is a cypress (*Taxodium mucronatum*), related to the Swamp or Bald cypress (*T. distichum*) of the southern United States. The trunk of this tree is 50 feet in diameter (14 feet larger than the diameter of the largest Sequoia). Its age was estimated by counting the annual rings of growth of smaller adjacent trees of the same species.

But, however long the period required, every living thing moves steadily on from its initial, one-celled condition, through stages corresponding to infancy, maturity, and old age, to inevitable death. Obviously, if life is to be continued, the individuals must function, not only for themselves, but for the race to which

[1] The Aldabra tortoise (*Testudo sumeirei*) was brought to England from the island of Mauritius in the summer of Queen Victoria's diamond jubilee (1897). It is known to have been kept on the island of Mauritius for 160 years, and previous to that time lived on the island of Aldabra, where it was noted as being of unusual size. (*All about animals.* George Newnes, Ltd. London, 1897.) There is record of a swan that lived to be 80, and one record of a parrot that lived to be some 150 years old. I am indebted to Dr. F. A. Lucas for these data and the citation.

they belong; they must provide for *the production of new individuals.* This is known as *reproduction.*

The Essence of Reproduction.—From the standpoint of function or physiology, the essence of reproduction is getting a new start; from the standpoint of structure *every new individual begins its independent life as a piece separated from a pre-existing individual,* and the process always involves the sacrifice of all or of a portion of itself by the parent organism. For the offspring, reproduction means *rejuvenation;* for the parent it means *senescence.*

Perpetual Embryogeny.—In plants we have the interesting condition of a tissue, like the growing points of stems and roots and the cambium layer of woody stems, where the cells retain their power of reproduction throughout the life of the individual. The cells of woody tissue, for example, are never obtained by the cell-division of pre-existing xylem, but always by the division of cambium cells, while the cambium retains its embryonic character and its power of reproduction as long as the individual remains alive. But eventually the individual, as a result of environmental and other influences, grows old and dies. We see a striking illustration of this in the case of apple trees in an old orchard. Almost, if not quite, within the lifetime of a man they pass from vigorous saplings, through a period of maximum vigor and bearing, to a condition of obvious old age, and cease to be profitable bearers (reproducers), and must be replaced with new stock from the nursery.

Types of Reproduction.—Broadly speaking, there are two main types of reproduction, one involving only cell-division, the other involving both cell-division and cell-fusion. All variations of the former are grouped under the heading of *asexual reproduction;* cell-fusion is a process of *sexual reproduction.* In this chapter we shall consider only types of asexual reproduction.

Types of Asexual Reproduction.—In asexual reproduction the individual may give off either a single cell or a multicellular portion of itself. The latter process may be either *natural* (by the formation of tubers, bulbs, and other reproductive structures), or *artificial* (by layering, cuttings, cions for grafting, etc.). A single cell, given off by the plant as a reproductive body, is called

a *spore*, though in certain cases the term is applied to structures of more than one cell. The various types of reproduction are shown in tabular form as follows:

- **Reproduction**
  - **Asexual**, involving cell-divisions only
    - 1. By giving off special reproductive bodies of one or few cells called *spores*
    - 2. By giving off multicellular portions of vegetative tissue
      - *a.* **Natural** (tubers, bulbs, etc.)
      - *b.* **Artificial** (layering, cuttings, etc.)
  - **Sexual**, involving cell-fusions

By some writers the term asexual reproduction is confined to reproduction by spores, while reproduction by layering, cuttings, tubers, bulbs, leaves, etc. is called *plant propagation*. This distinction, however, is more or less arbitrary and artificial, as no hard and fast line can be drawn between the different methods, but the latter term is in general use, especially among gardeners and nurserymen.

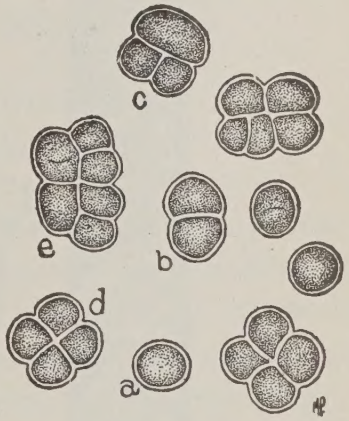


FIG. 194.—Individual plants of green slime (*Pleurococcus vulgaris*), showing the tendency of the cells to remain attached after cell-divisions, thus causing transitions from a one-celled to a multi-cellular plant.

Asexual Reproduction in the Lower Plants.—It is not possible here to treat with any approach to completeness the methods of asexual reproduction in non-flowering plants, but a few cases will be noted to emphasize the essentials of the method.

a. By Simple Cell-division.—The simplest type of reproduction is found, naturally, in the most simply organized plants, namely, the bacteria, which are one-celled plants. As the name of the Class (*Schizomycetes*, Fission-fungi) to which they belong implies, reproduction, with certain exceptions, consists in the division of this one cell (the *mother-cell*) into two *daughter-cells* (Fig. 142). The two daughter-cells do not, usually, remain attached; they separate, each becoming an independent new individual. In

such a case the parent cell loses its existence as an individual. A similar type of reproduction is found in the simple green alga, *Pleurococcus vulgaris*, which grows on the bark of trees, on moist walls and boards, and in other cool, moist, shady locations.

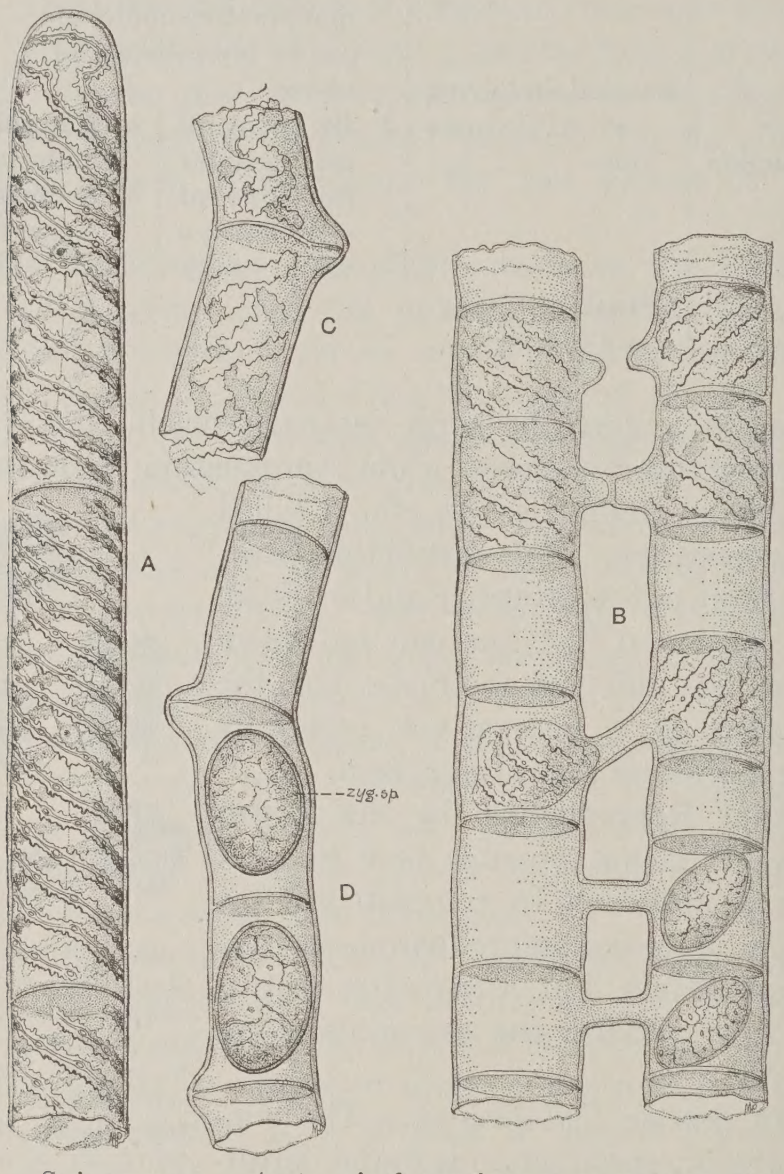


FIG. 195.—*Spirogyra* sp. *A*, terminal portion of vegetative filament; *B*, stages of scalariform conjugation; *C*, preparation for lateral conjugation; *D*, zygospores formed by lateral conjugation.

Like the bacterium, a single plant of *Pleurococcus* is too small to be seen by the unaided eye (Fig. 194).

Often, in bacteria and algae, the daughter-cells, after division, remain attached, either temporarily or permanently, forming

a cellular aggregate. In *Pleurococcus* the daughter-cells adhere in such a manner as to form a *superficial aggregate.* In some bacteria and algae (*e.g.*, *Spirogyra*) the cells adhere end to end, forming a thread-like *linear aggregate.* These temporary and permanent linear and superficial aggregates mark a structural transition from one-celled (*unicellular*) to many-celled (*multicellular*) organisms (Figs. 194 and 195).

The life history of *Pleurococcus* may be represented by the following outline.

OUTLINE OF LIFE HISTORY OF PLEUROCOCCUS

Unicellular plant
↓
Cell-divisions
↓
Temporary cell-aggregates
↓
Separation of daughter cells
↓ ↓ ↓ ↓
Unicellular plant | Unicellular plant | Unicellular plant | Unicellular plant

b. By Budding.—The yeast plant, instead of dividing into two new plants, reproduces by a process known as "*budding.*" Under certain conditions, as yet not well understood, a small area of the cell-wall becomes less resistant than the remainder and, as a result of the internal turgor pressure, the cell bulges at that point, forming a primitive sprout or *bud.* Eventually the bud becomes detached from the parent cell, and continues as a new plant (Fig. 89).

In some of the Liverworts and Mosses multicellular buds, known as *brood-buds* or *gemmae,* are often formed (Figs. 196 and 197).[1]

c. By Spores.—Among *bacteria* and *algae,* especially under conditions of unfavorable environment, the protoplasm organizes a new cell or cells within the wall of the mother-cell. Commonly each cell organizes only one spore, and the spores are usually much

[1] In various Liverworts vegetative reproduction results from tips of the thallus becoming isolated by the dying of older tissue back from the tips, thus producing new individuals.

more resistant than the mother-cell to extremes of temperature and to poisonous substances like disinfectants. They may retain their vitality for years, and this fact, combined with their resistance, makes it very difficult to secure disinfection or sterilization when the bacteria are in the condition of spores. Thus milk may readily be *Pasteurized* by heating it for 20–30 minutes at 70° C. and then rapidly cooling it; but this treatment will not destroy bacterial spores, and is only effective, therefore, in

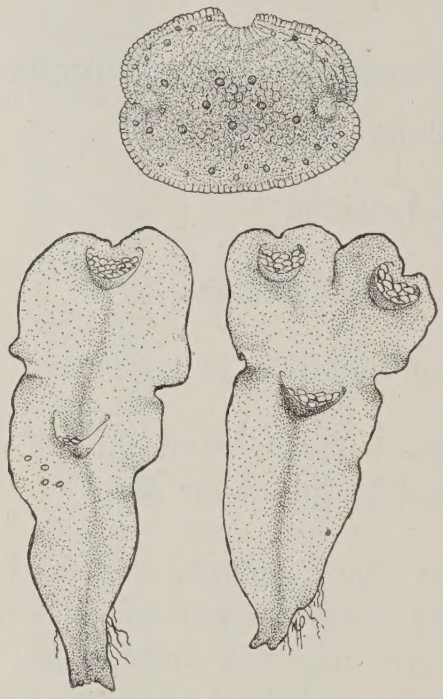


Fig. 196.

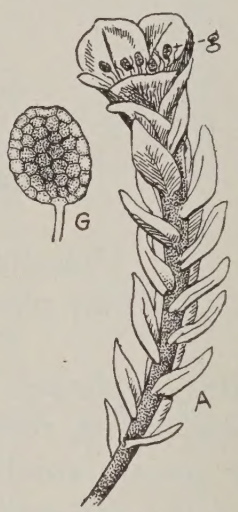


Fig. 197.

Fig. 196.—A liverwort (*Lunularia*). Below, portions of the thallus, showing the lunar-shaped cupules, with brood-buds, or gemmae. Above, a single gemma, greatly magnified. (Cf. Figs. 197 and 386.)

Fig. 197.—A moss (*Tetraphis*), showing gemmae; *G*, a gemma enlarged. (Cf. Figs. 196 and 386.)

destroying species that do not form spores, or those in the sporeless state, thus insuring only partial sterilization.

The protoplasm of yeast cells, especially when the yeast is grown on a solid medium and at a comparatively low temperature (*e.g.*, 30° C.), divides into four (or some other multiple of two) cells, within the wall of the mother-cell, which thus functions as a sac or *ascus* to hold the *ascospores*. In view of this mode of reproduction yeast is classed as one of the sac-fungi or *Ascomycetes*.

The reproduction of mosses, ferns, and fungi by spores is discussed in connection with the life histories of those plants.

Artificial Propagation.—Artificial vegetative propagation depends upon the power of certain tissues to retain their embryonic or *meristematic* nature, and the characters which come to expression depend largely upon the environment. Thus, when a cambium-cell divides, one of the two sister cells (inside the cambial ring) becomes transformed into xylem; on the outside of the cambial ring the cells become transformed into cortex or

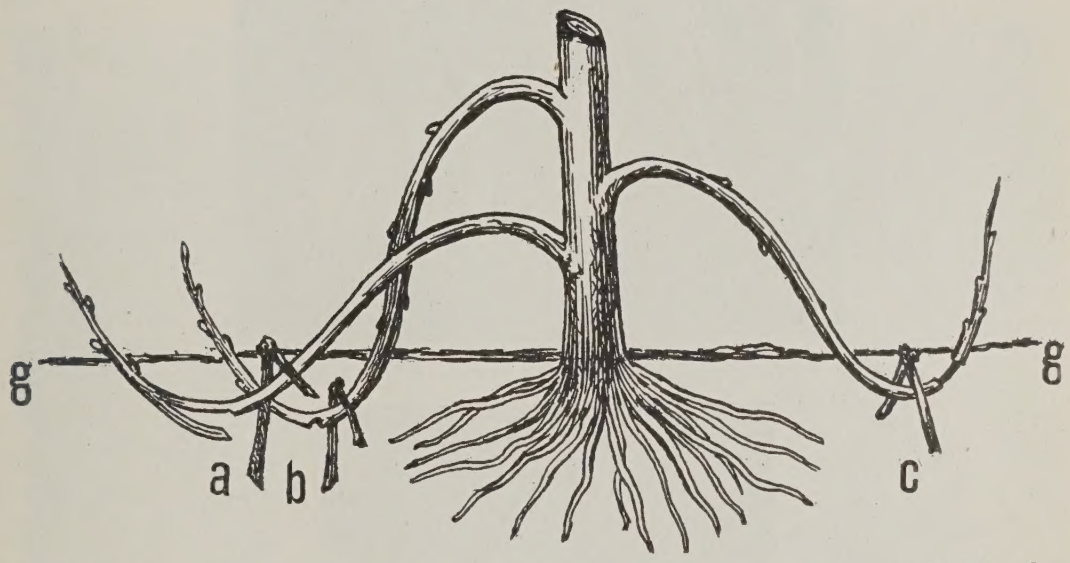


FIG. 198.—Methods of layering: *a*, by tongueing or heeling; *b*, by notching; *c*, by ringing or gridling; *g–g*, surface of ground.

ultimately into bark, because the conditions (the environment) within the tissues are different in the two cases.

a. Layering.—In the process known as *layering,* cells which would normally develop stem tissue have the expression of their inheritance altered by exposure to external influences (such as contact with soil, air, water, and light) and changes in nutrition, and they develop root-tissue and roots. Layering is accomplished by bending a branch over to the ground, and pegging it down so that a portion is beneath the surface. In the course of time roots will develop from the buried portion, and this result may be hastened by twisting, notching, tongueing, or girdling the stem (Fig. 198). This treatment interferes with the downward passage of sap in the cortex, and the plant food dissolved in the

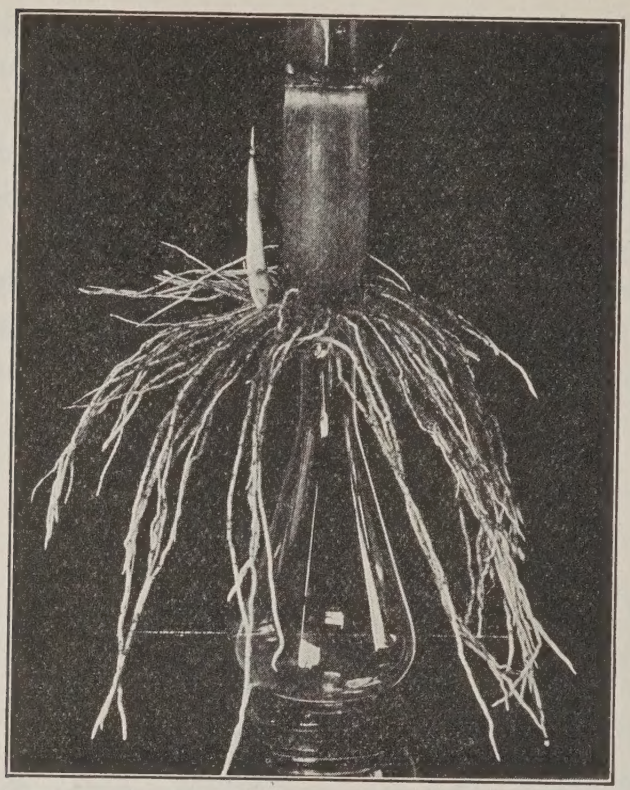


FIG. 199.—Fibrous roots on a cutting of sugar cane.

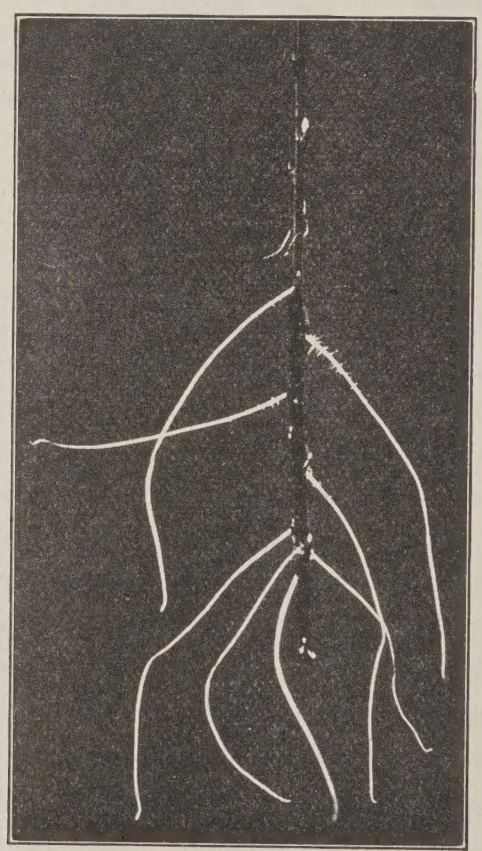


FIG. 200.—Branch of a willow (*Salix* sp.), showing the formation of fibrous roots. The lower portion of the stem was placed in water for a few days.

sap accumulates above the cut, thus stimulating the formation of new organs such as the roots. Ultimately the branch with its new roots may be completely severed from the parent plant, and become established as a new individual.

b. Cuttings.—If a piece is cut from the stem of a plant such, for example, as willow or sugar-cane, and the freshly cut end placed in water or in moist sand, roots will develop from that end or from various points above, while from the portion of the "cutting" in the air new buds will develop, or dormant buds will become active and give rise to new stem parts, or to a new shoot

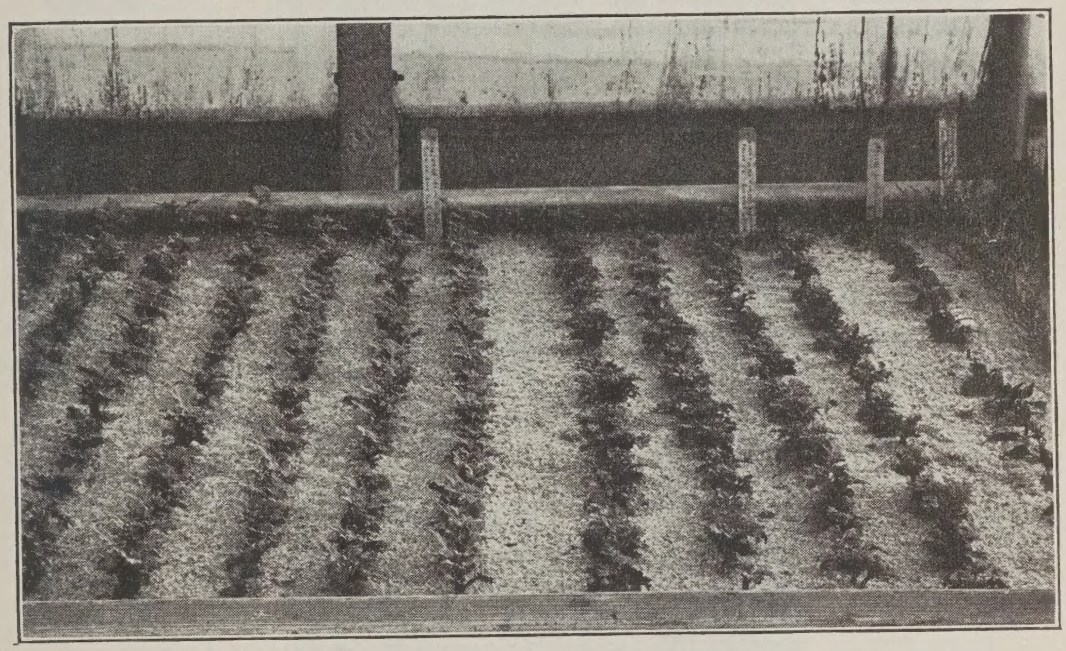


FIG. 201.—Portion of a propagating bench, showing stem-cuttings of Chrysanthemum.

(Figs. 199–200). House plants, such as geraniums and many others, are commonly propagated in this way. Figure 201 shows a sand bed in a propagating house, with hundreds of stem-cuttings rooting in moist sand. The process is facilitated by plenty of moisture in the soil and in the air above it, and by *bottom heat,* underneath the propagating bench. Preliminary to root-formation on woody cuttings, parenchymatous or wound tissue (*callus*) develops on the freshly exposed surface of the cutting in the sand, and the new roots arise from the callus (Fig. 202).

c. Leaf Propagation.—Many plants are propagated by leaves treated as stem cuttings. This is the common method of repro-

duction of various species of begonia (Fig. 203). With the leaves of a potato plant it has been found that the results are uncertain. Sometimes the cut end of the petiole will develop roots, or again it will develop tubers or tuberlike enlargements, with or without roots (Fig. 204). This case, however, has only theoretical interest, since the "potatoes" themselves—the tubers—afford

FIG. 202.—Stem-cutting of *Diervilla*, removed from the sand of the propagating bench to show the callus on the cut surface. The new roots will develop on this callus.

every advantage essential to successful propagation. The potato tuber, in fact, and also layering, illustrate the transition from artificial to natural propagation.

d. Grafting.—When the freshly cut surfaces of two living branches are brought into close contact under favorable conditions they will grow together, becoming as one stem. This practice is one of the oldest methods of plant propagation known

to horticulture. The rooted plant is the *stock*, the cutting to be attached is the *cion;* the process of bringing them together is commonly called *working*. They must be placed together so that the cambium (embryonic) layers of each are in contact,

FIG. 203.—Young plantlets developing from the edges of lacerations (*e.g.*, *s*) made in a large leaf of Rex begonia.

and the two must be firmly bound to prevent slipping. The region of contact must also be protected from the air and the spores of fungi by a coating of grafting wax. Various methods of grafting are illustrated in Fig. 205.

FIG. 204.—Regeneration at the leaf-base of potato leaves (*Solanum tuberosum*). *a*, roots formed; *b*, tuber-like enlargement; *c*, same as *b*, with roots; *d*, formation of true tuber. (After Miss Elsie Kupfer.)

Cion and stock must be of the same or closely related species (Fig. 206). Many of the horticultural varieties of shrubs and of fruit and nut trees (*e.g.*, lilacs, apples, walnuts, etc.) are propagated almost exclusively by being grafted on to a rooted stock of

FIG. 205.—Various methods of grafting. (1) Root grafting in its different stages. *a*, Cion cut for insertion; *b*, stock prepared to receive the cion; *c*, stock and cion united; *d*, the same tied up with waxed cord. (2) Cleft grafting (Herbaceous). *a*, Cion ready for insertion; *b*, stock; *c*, stock and cion united; *d*, the same tied up with raffia; *e*, cleft grafting (woody). Stock with two cions. (3) Saddle grafting. *a*, Cion; *b*, stock; *c*, cion and stock joined. (4) Budding. *a*, Budstick; *b*, T-shaped cut in bark of stock; *c*, bud ready for insertion; *d*, stock with bud inserted; *e*, the same tied up with raffia. (From Brooklyn Botanic Garden Leaflets.)

some related species. Apple varieties are commonly propagated by working cions on seedling roots (root-grafting). The umbrella catalpa is produced by grafting the bushy *Catalpa bignonioides*, var. *nana* on to *Catalpa speciosa* stock. The stocks do not increase in height.

FIG. 206.—A tomato (*Lycopersicum*), grafted on a potato (*Solanum*). Note the potato tuber on the surface of the soil.

Among the purposes of grafting are the following:

1. *To Increase the Speed of Propagation.*—Mature, bearing trees of commercial fruits and nuts may be obtained more rapidly this way than by any other method.

2. *To Perpetuate a Variety.*—This is necessary where plants do not bear seeds (*e.g.*, navel oranges), where the seeds do not germinate readily or well, or where the seeds do not "come true."

3. *To Substitute More Desirable for Less Desirable Varieties.*—A vineyard of a low-yielding or otherwise unprofitable variety of grapes may, in a brief period, be transformed into one of a more profitable variety by grafting cions of the better variety on the old stock, and pruning away the undesired parts.

4. *To Produce Some Marked Change in the Nature of the Cion,* such as rendering it more dwarf, more fruitful, or more robust (some

FIG. 207.—Bridge-grafting where a tree has been girdled. (After Fletcher. U. S. D. A. Farmers' Bull. No. 710.)

roses and grapevines). When apple cions of large-sized trees are grafted on stock of Paradise, a small growing tree, the cion is dwarfed because its food supply is not sufficient to produce a normal sized tree.

5. *To Adapt Plants to Various Climates or Environments.*—For of example, the plum is commonly worked on peach roots in the southern United States since the peach thrives better in sandy soils. Varieties of cultivated apple are worked on Siberian crab,

as the roots of the latter can better withstand the long and severe Siberian winters. To these five may be added a sixth, namely:

6. *To Combat Destructive Plant Pests.*—For example, varieties of the Old World grape (*Vitis vinifera*) are worked on stock of varieties of the New World grape (*V. labrusca*) as a means of

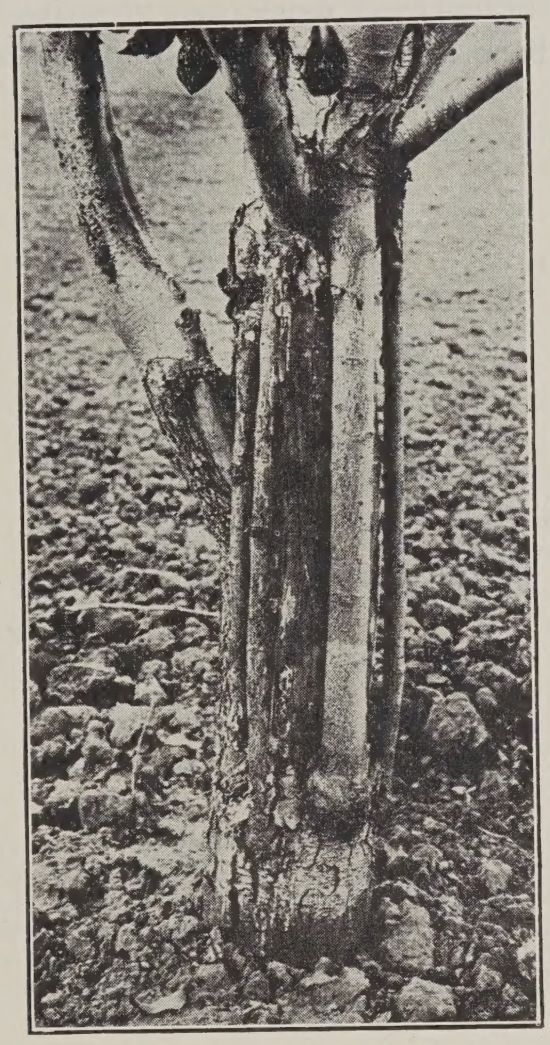


Fig. 208.—Bridge-graft three years old on a pear tree that was girdled by blight. (After Fletcher. U. S. D. A. Farmers' Bull. No. 710.)

combating the root-louse (*Phylloxera*), which does not infest the roots of the New World grape.

Bridge Grafting.—One of the most interesting types of grafting is *bridge grafting.* It is not unusual for apple trees and other fruit trees to be severely injured in the winter by being girdled by mice and rabbits that gnaw the bark. This happens especially when the lower portion of the trunk is surrounded by tall

grass or weeds which afford a congenial shelter for the animals. The trees may also be similarly injured by boring insects and by implements used to till the soil around the tree and, in the case of pear trees, by blight. The life of the tree can then be saved only by bridging over the girdled area. This is done by using pieces of small branches as cions, and inserting the ends under the uninjured bark at opposite sides of the wound, in such a

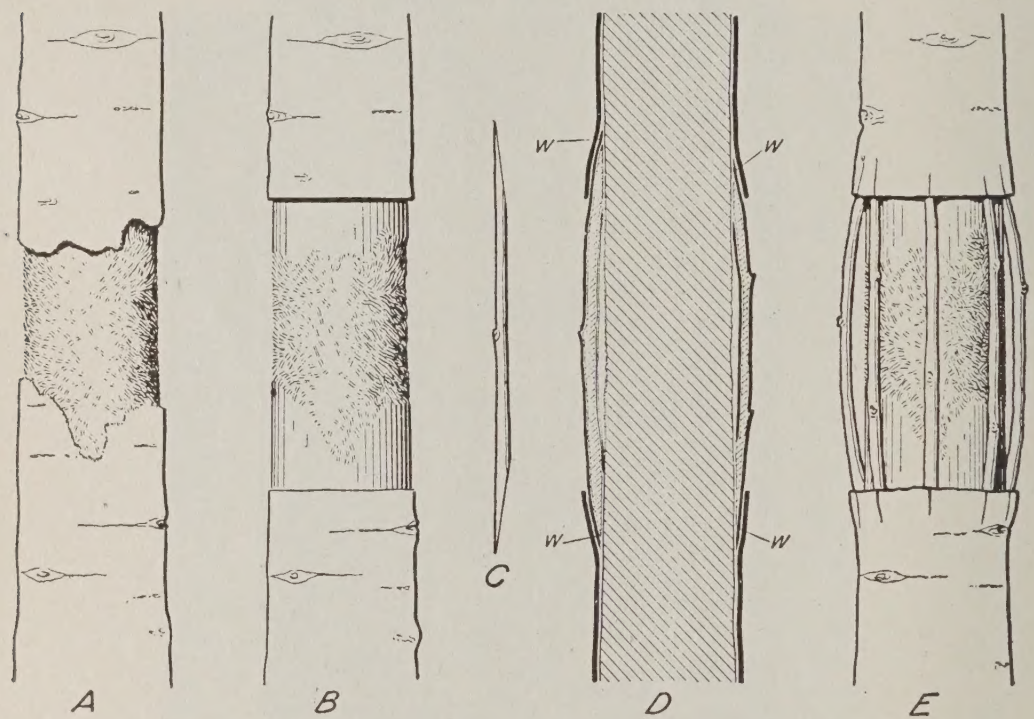


FIG. 209.—Details of bridge grafting: A, trunk of a tree girdled by mice; B, the wound cleansed and the bark along the margins trimmed back to healthy growing tissue; C, a cion with beveled ends ready for insertion; D, longitudinal section of the trunk with cions in place, showing their insertion under the bark of the trunk (*w*); E, cions in place ready for waxing. (After Yerkes. U. S. D. A. Farmers' Bull. No. 1369.)

way, of course, as to bring into contact, at each end, the cambium layers of both cion and stock (Figs. 207–209).

e. Budding.—Budding is a kind of grafting. A small piece of bark and underlying cambium tissue, bearing a bud, is sliced from a branch and inserted into a slit in the bark so that the cambium of cion and stock are brought into contact. Binding and waxing are practiced as in grafting (Fig. 205, (4)). Budding is the common method of propagating most stone fruits, such as plum and peach. In Florida, oranges are propagated almost entirely by budding. One- or two-year-old seedlings of commercial varieties

are budded on stocks of sour orange (*Citrus Aurantium*), rough lemon, grapefruit, or the trifoliate orange. The different stocks are adapted to different environments and different varieties.

Natural Propagation.—In natural propagation the reproducing member is separated from the plant without the intervention of man. There are various methods of this, as follows:

a. By Layering.—Propagation by layering often takes place without the intervention of man. In such cases the branches become prostrate and in contact with the soil by their own weight, or by other accidental circumstances.

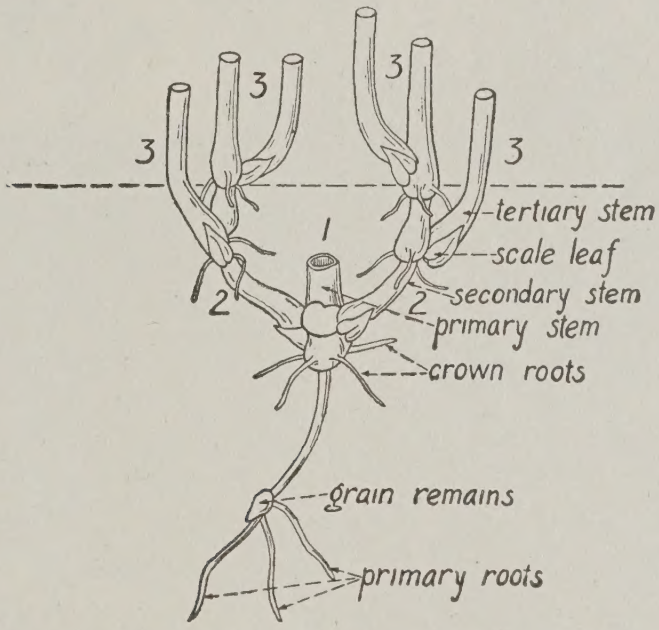


Fig. 210.—Tillering in cereals. Diagrammatic. (From Robbins, after Schindler.)

b. By Tillering.—After the first vertical stem or stool is formed in cereals and other grasses, lateral branches are commonly formed near the surface of the soil; these at first, grow horizontally and produce roots where their joints come in contact with the soil (Fig. 210). From one "stool" as many as 50–100 branches may be formed, each bearing grain; usually there are only five or six. The number depends upon the species (oats, for example, tiller less than barley or wheat), upon the variety, and upon external conditions. Plants in shade, or poorly nourished, do not tiller as much as those in better light, hence a thin stand promotes tillering. If the crop desired is hay or straw then varieties should be chosen that naturally tiller freely, and this

should be encouraged by cultural conditions. Where tillering is abundant the grain crop is usually not so good in either quantity or quality.

c. By Suckers.—In many plants, such as the raspberry, rose, Japanese knotweed (*Polygonum Sieboldii*), and others, branches arise from underground stems and grow up through the soil into the air (Fig. 211). Roots develop at the underground nodes of these branches, which commonly become separated from the

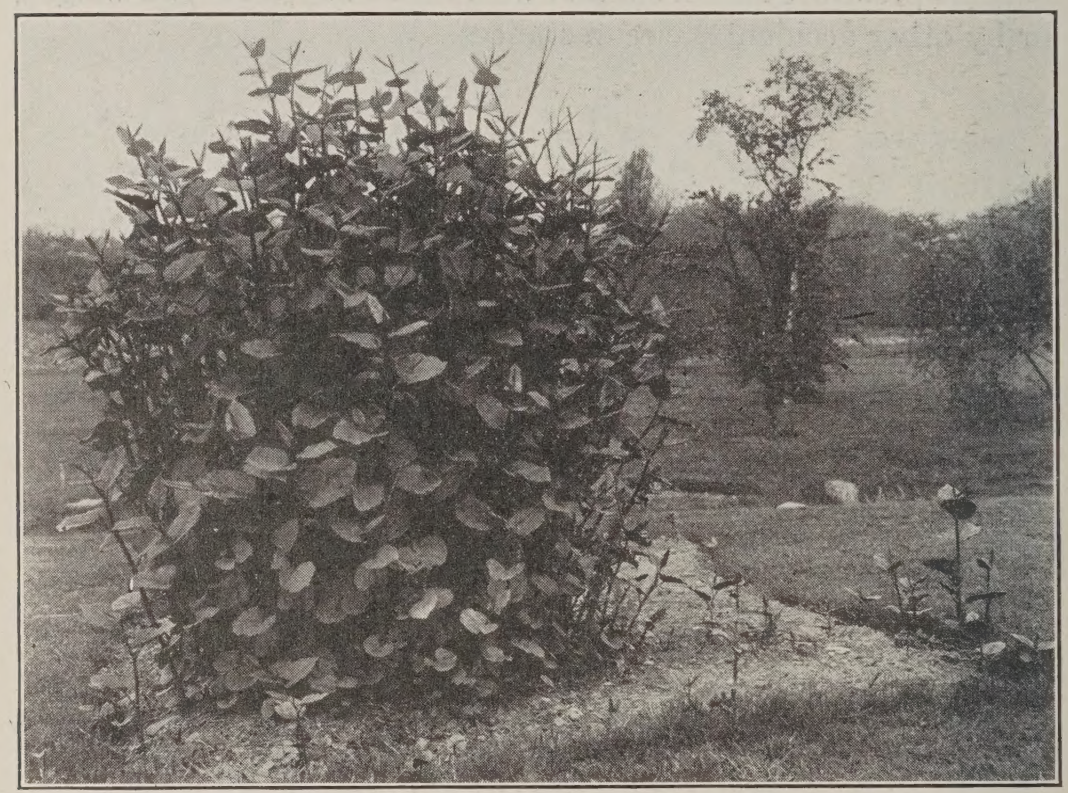


FIG. 211.—Clump of Japanese knotweed (*Polygonum Sieboldii*) with adjacent suckers which arose from underground rootstocks.

parent stock and continue as independent plants. Such plants are very difficult to eradicate, and often become very troublesome in lawns.

d. By Stolons.—In strawberries, the Boston fern, and numerous other plants, branches, called runners or *stolons*, arise above ground and trail or bend over so as to bring their tips in contact with the moist surface of the soil. Roots and finally a shoot system develop at the tip of the stolon, and thus a new plant becomes established (Fig. 212). Some plants, such for example,

as the Houseleek (*Sempervivum tectorum*), develop short stolons which produce small shoots at the tip, even before this is brought

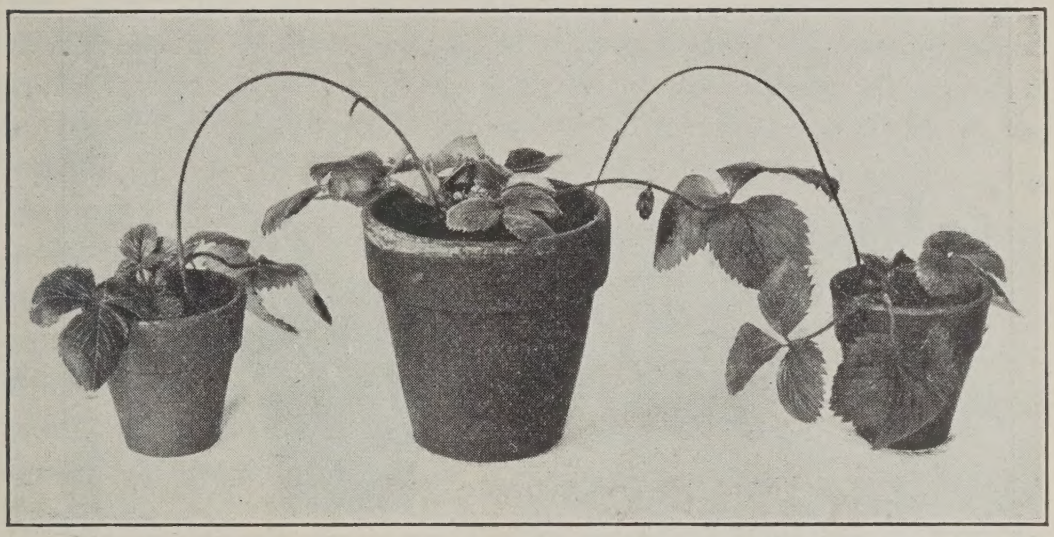


FIG. 212.—Propagation of strawberry (*Fragaria*) by stolons ("runners"). The two plants in the small pots developed from the tips of the stolons produced by the older plant in the central pot.

FIG. 213.—*Sempervivum tectorum*, with stolons.

into contact with the ground. Such structures are called *offsets* (Fig. 213). Some plants (*e.g.*, *Chlorophytum elatum* and Eel-grass) develop stolons which produce new plants, not only

at the tip, but also at points back from the tip, sometimes before touching the ground (Figs. 214, 215).

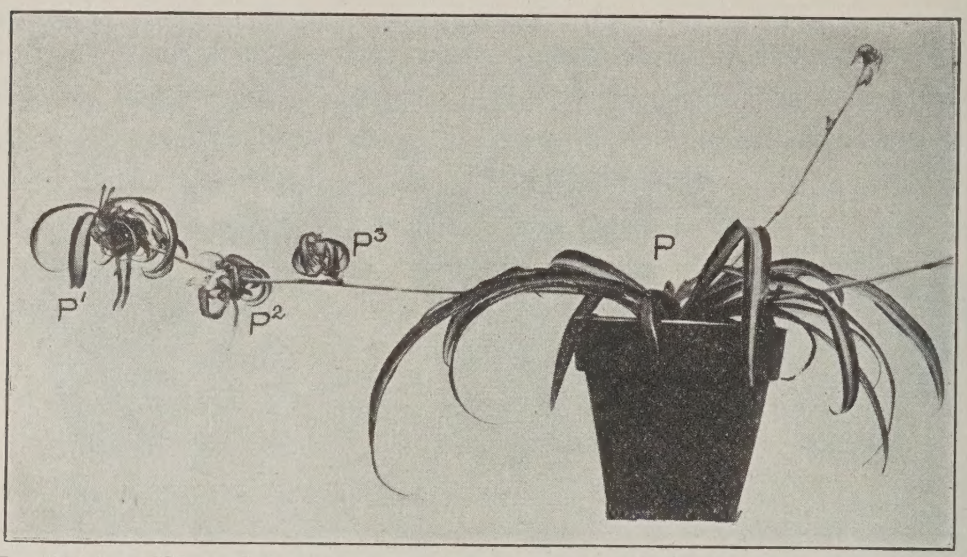


FIG. 214.—*Chlorophytum elatum*, showing vegetative propagation by runners. P^1, P^2, P^3, new plants; P, parent plant. From P^2 one root, and from P^1 two roots hang down.

e. By Rootstocks.—A rootstock or *rhizome* is a creeping underground stem, growing more or less horizontally, and usually

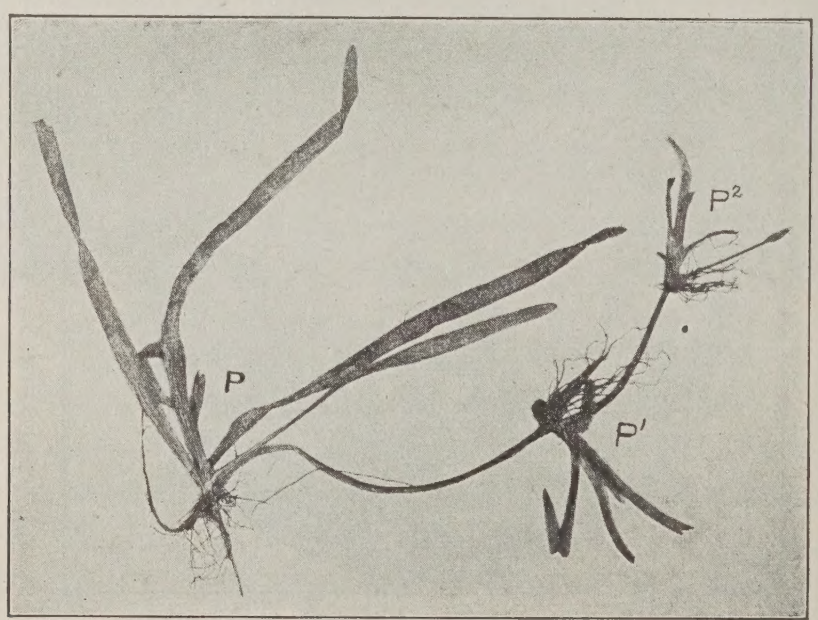


FIG. 215.—Eel-grass (*Vallisneria spiralis*), showing vegetative propagation by stolons. Young plants at P^1 and P^2.

somewhat scaly. It bears the scars where the above-ground stems of previous years were attached, and develops numerous

roots from its under surface. In some plants, *e.g.*, Wake-robin (*Trillium*), Solomon's Seal (*Polygonatum*, Fig. 70), and others, the rootstocks are comparatively short and thickened with stored food; in other plants, *e.g.*, the Sedges (*Carex*), various grasses, the bracken fern (*Pteridium aquilinum, et cetera*, it is long and slender, and often, as in couch grass (*Agropyron repens*), jointed. The rootstock is the means through which many plants are perennial, and, in the case of weeds, this renders their extermination very difficult, for every time the rootstock is cut a new individual plant is started. The leafy spurge (*Euphorbia Esula*), a European weed, resembling the cypress spurge and spreading by a creeping rootstock, has recently, in certain parts of the United States, became a serious menace to pastures and meadows, and to such crops as corn and oats, and organized efforts are being made to eradicate it.

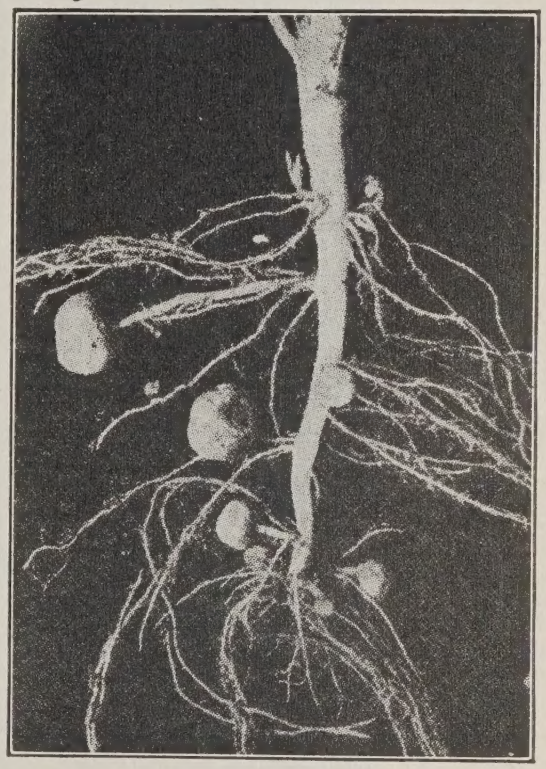


FIG. 216.—Potato (var. Irish Cobbler) showing the formation of tubers at the tips of underground stems. Cf. Fig. 512. (After C. F. Clark, U. S. Dept. Agr.)

The stems of some plants are somewhat transitional between a true rootstock and the *tuber*, next to be mentioned. This is illustrated by the tuber-like rootstocks of the Indian cucumber (*Medeola virginiana*); green-brier (*Smilax rotundifolia*), with long, sparingly tuberous rootstocks; carrion-flower (*Smilax herbacea*), with numerous short thick tubers; and others (Figs. 499, 636).

f. By Tubers.—The potato plant forms slender, underground stems, the tips of which enlarge as organs for the storage of food (Figs. 216, 508). These enlarged tips are the tubers or "potatoes" of commerce. That they are modified stems may be seen by watching their development, and also by careful examination of them when mature. At one end (the proximal end) may be seen the *scar* where the tuber was attached to the slender portion

of the runner, while the *eyes* will be seen to be undeveloped lateral branches or buds, commonly three together, in the axils of modified, scale-like leaves, usually so greatly reduced as hardly to project at all from the surface of the tuber (Fig. 518). The eyes are arranged on the tuber in a spiral, usually turning to the

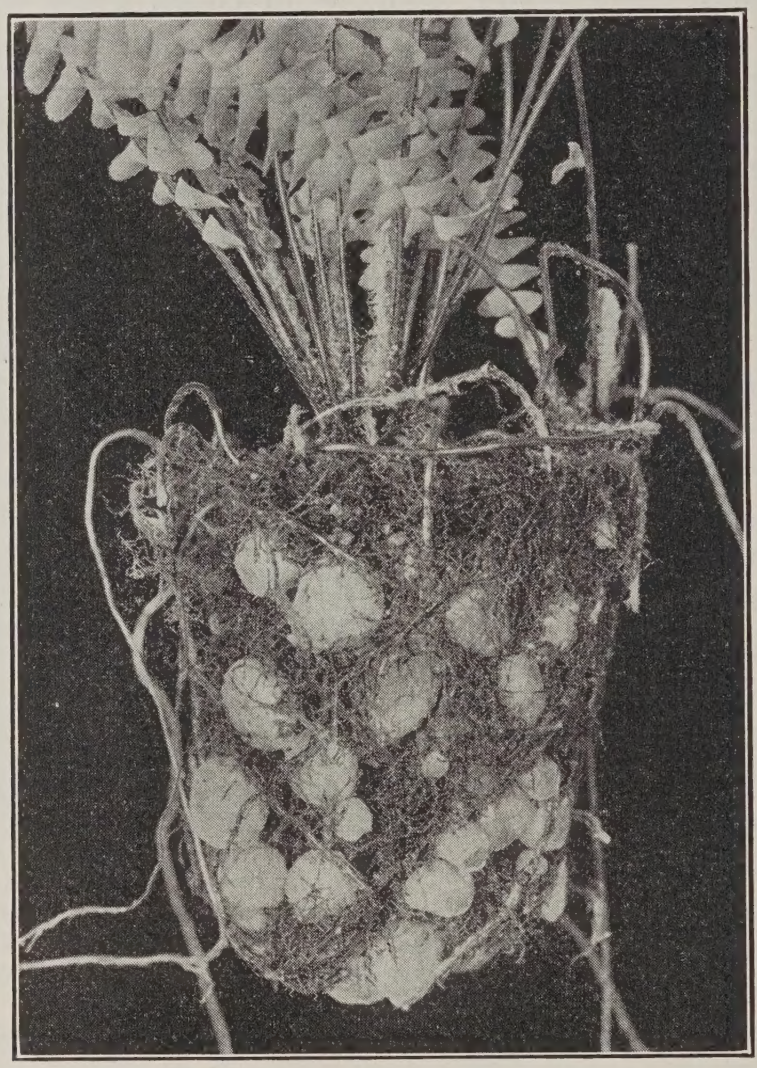


FIG. 217.—Portion of a fern, *Nephrolepis cordifolia* (*N. tuberosa*) removed from a pot in which it had been growing and showing the numerous tubers. Several stolons or "runners" are also seen branching from the main stem near the surface of the soil. (Cf. Fig. 67.)

left, though right handed spirals have been recorded. When potato tubers are planted they are usually cut into several pieces, but care must be taken to have an eye on each piece.

After the tuber is planted, the enzyme, diastase, which has gradually been formed in every cell during the period of storage,

begins to convert the insoluble starch into sugar. The sugar is then dissolved and begins to flow toward the eyes or buds, which gradually resume their activity and growth, at first depending entirely upon the nourishment stored in the tuber. As soon as roots develop, the new plant begins to absorb moisture and mineral food-elements from the soil.

Under certain abnormal conditions potato tubers are formed on aerial stems (Fig. 109).

Other Tubers.—Other familiar examples of tubers are found in one of the sunflowers, *Helianthus tuberosus*, the tuberous begonias, and in the fern *Nephrolepis cordifolia* (*N. tuberosa* of the florists), related to the Boston fern, and in other ferns (Fig. 217). Certain plants, such as the sweet potato, have tuberous roots, but these are not true tubers.

g. By Corms.—We have just seen that tubers are enlargements of the *tips* of stolons. In some plants the *base* (instead of the tip) of the stem serves as an organ for food storage and propagation. In this case the organ is called a *corm;* it is usually covered with a few scale-like leaves. Illustrations are found in gladiolus, crocus, colchicum, Indian turnip (*Arisaema triphyllum*) adder's tongue (*Erythronium*), and other plants (Fig. 218, F–H).

h. By Bulbs.—Like tubers and corms, a *bulb* is a modified stem, but differs from the former in the fact that the food is stored chiefly in leaves or leaf-bases, which comprise the main bulk of the structure; the stem portion is short. In a *tunicate bulb*, like the onion and hyacinth, the leaf-bases are concentrically arranged (Fig. 218, A). The scales of tulip bulbs are entire leaves. In a *scaly bulb*, like the lily, the scales overlap like shingles, *i.e.*, they are *imbricated* (Fig. 218, B). In "multiplier" onions the bulb develops in separable parts called *bulbils* (Fig. 218, D).

Not to increase examples, the tulip may be chosen to illustrate the growth of a plant from bulb to bulb. A stem is modified into a bulb by the failure of the internodes to elongate, *i.e.*, the stem does not grow in length, while at the same time it does grow in thickness as a result of the storage of nourishment, chiefly in the form of a carbohydrate, such as starch. Most of the nourishment, however, accumulates in the leaves attached to the nodes of the stem. While these changes are going on, the growing point at the tip of the abbreviated stem-axis develops an embryonic

stem, at the apex of which is the flower bud. In the formation of the tulip bulb the stem grows eccentrically, and the scales develop in such a way as to form an angle of about 45° with the stem (Fig. 219, (21)).

Tulip bulbs are usually planted in the fall at a depth of 5–6 inches, and the next spring the internodes of the embryo stem in the center elongate rapidly and uniformly, sending up leaves and the long flower stalk with its terminal blossom. In certain cases and under certain circumstances, especially with seedlings, the

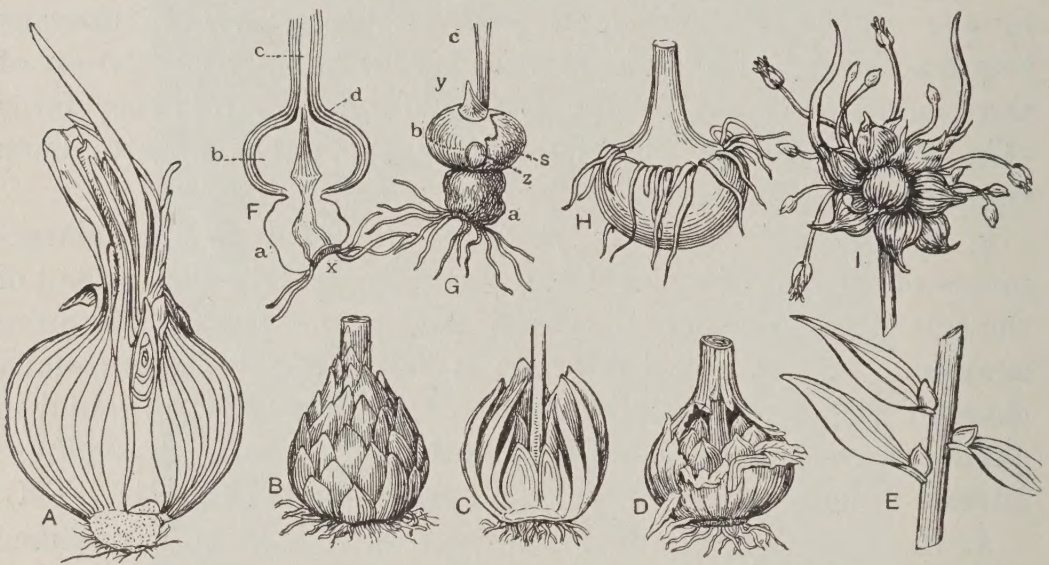


FIG. 218.—A, tunicate bulb of Onion (*Allium Cepa*), in longitudinal section; B, Scaly bulb of Canada Lily (*Lilium canadense*); C, Same as B, but in longitudinal section; D, Bulb of Garlic (*Allium* sp.) with portion of the scales cut away so as to disclose the young bulbs within; E, Portion of stem of Tiger Lily (*Lilium tigrinum*), showing bulbils in the axils of the leaves; G, Corm of Crocus showing a terminal and one lateral bud. The horizontal lines represent the scars of the few scales that have been removed. At the base is the remnant of last year's corm. The various buds will develop into new corms. F, Vertical section of a similar corm. H, flat corm of Cyclamen; I, Bulblets at the apex of a flower stalk of the Onion. (Redrawn with modifications, from various sources.)

axis elongates downward as well as upward, producing what is known as a "*dropper*," or "*sinker*," which is part stem and part leaf (Fig. 219, (2 and 3)). The sinker is hollow, and at its lower extremity there develops another bulb, often three or four inches below the parent bulb. In addition to sinkers, there frequently develop *offsets*, which are bulbs formed as lateral branches of the main bulb.

i. By Buds.—In addition to corms and bulbs (which are really subterranean buds), there are numerous forms of aerial

buds. A bud is always an undeveloped stem or branch, in which the internodes have not elongated. Commonly the bud, as it develops, remains attached to the plant that bears it, forming a

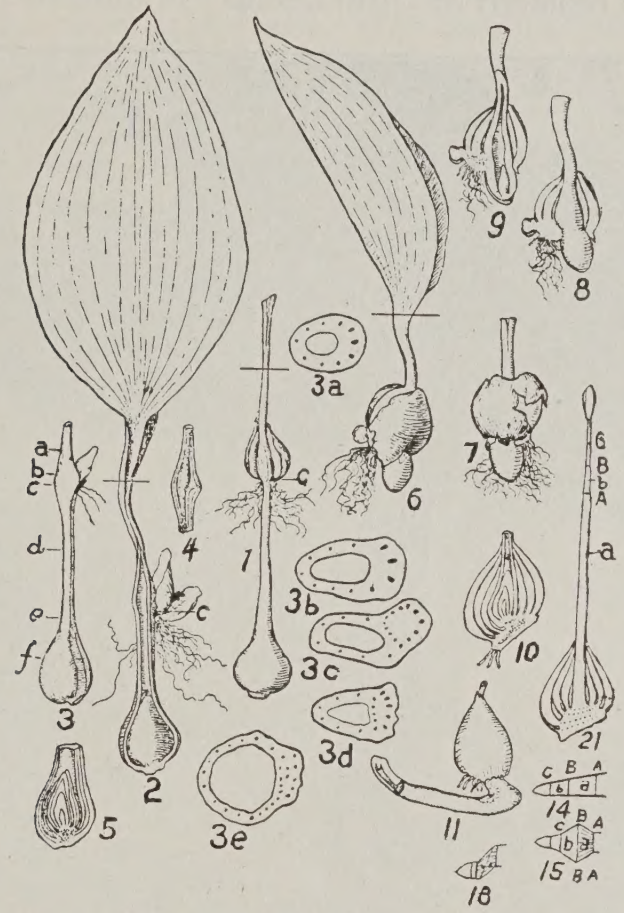


FIG. 219.—Reproduction of tulips by bulbs. 1, Portion of tulip plant, showing the "dropper" extending down from *c*. The horizontal line in each figure represents the surface of the soil. 2, An entire plant with the dropper shown in longitudinal section. Note that it is hollow and bears a new bulb enclosed at the base. 3, external view of stem portion of dropper with lateral bulb projecting at the right above the roots. The letters *a–f* represent the levels at which were cut the sections shown in 3*a*-3*e* (3*f* not shown). The sections show the distribution of the vascular bundles. 5, longitudinal section of base of dropper and the enclosed new bud. 6 and 7, Views of a plant collected March 22, showing a dropper just emerging from the old bulb, and also a small lateral bulb. 8, Same with old bulb sectioned; 9, Same with dropper also sectioned. 10, Longitudinal section of an old bulb in early spring, showing the eccentric radial growth of the stem and the position of the bulb in the soil. 11, Plant with dropper growing horizontally. 21, Flowering bulb of tulip, with scale leaves attached to closely compacted nodes. The flower stalk (with flower bud at top) has arisen by the symmetrical elongation of a few internodes, *a*, *b*, and *c*. A and B are nodes. Leaves not shown. (After Stout.)

lateral branch or (in the case of terminal buds) a new length of stem. Some plants, such, for example, as *Lilium bulbiferum*,

bear, in the leaf-axils of aerial stems, small buds, called *bulbils*, which drop off and become the starting point of new plants (Fig. 218, E). In the onion the flowers at the tip of the flower stalk are often replaced by "top onions" or bulblets (Fig. 218, I).

FIG. 220.—Lower portion of the trunk of a young tree of European Bird Cherry (*Prunus Padus*), showing numerous suckers developed from adventitious buds on the roots.

The essential structure of all buds is the embryonic branch, or stem, which may (as in the cases mentioned above) or may not be surrounded by modified leaves or portions of leaves. In the

latter event the bud is *naked.* Further illustrations of leafy buds are headed lettuce, the cabbage, and brussels sprouts, which serve, not so much to propagate new individuals, but to tide over the first season of drought (winter) plants which require two or more years to set seed. The familiar buds of trees and shrubs are also classed here. These may be either exclusively flower buds (golden bell or *Forsythia*, apple, cherry, etc.) exclusively leafy buds (maple, horsechestnut, and many others), or a

FIG. 221.—Yellow-flowered Alfalfa (*Medicago falcata*), showing new plants that have developed from true lateral roots. (After Garver. U. S. D. A. Dept. Bull. 1087.)

combination of the two (horsechestnut, lilac, and others) (Fig. 153).

In the willow (*Salix*), sumach (*Rhus*), cherry (*Prunus*), and many other trees, adventitious buds form on the roots, underground, and send up *suckers* which may in time become established as independent plants (Fig. 220). This is a regular method of vegetative reproduction of some of the alfalfas, and notably the yellow-flowered alfalfa (*Medicago falcata*), which has the most extensive root system of all the alfalfas (Fig. 221).

FIG. 222.—Leaves of *Bryophyllum crenatum*, reproducing by the formation of small plantlets at the notches of the leaf margin.

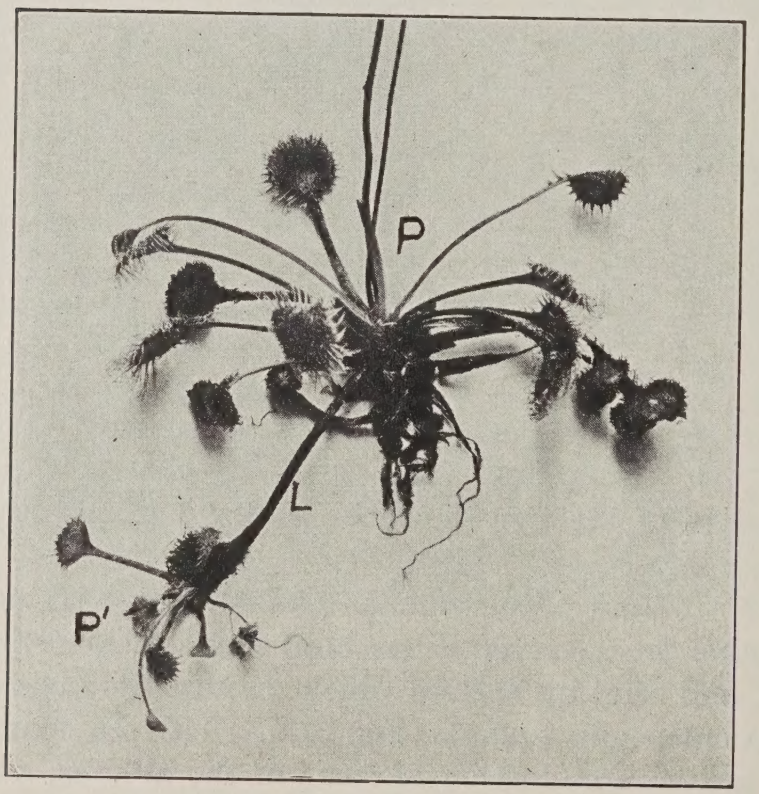


FIG. 223.—*Drosera rotundifolia.* Production of a young plant (P′) from the leaf of an older plant.

Naked buds may arise on any part of the shoot—branches, leaves, flower stalk, etc. They commonly differ from scaly buds, not only in the absence of bud-scales, but in not having a more or

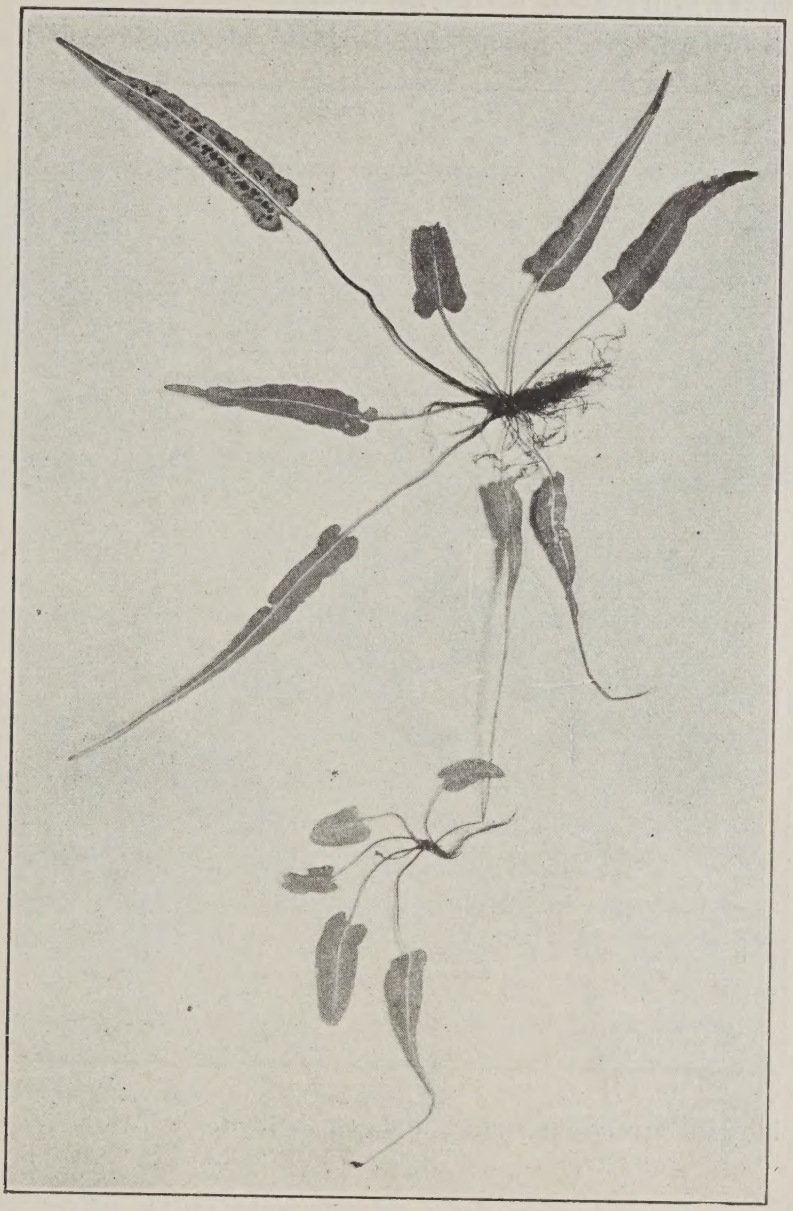


FIG. 224.—Walking fern (*Camptosorus rhizophyllus*). The smaller, lower plant originated at the tip of a leaf of the larger plant, and one of its leaves has, in turn, struck root.

less prolonged rest period. They are found in coffee, bigonia, gutta percha, chocolate, custard apple, and many other plants.

j. By Roots.—The fleshy roots of our numerous root-crops should be regarded, from the standpoint of the plant's economy,

as organs of propagation, serving to tide a biennial plant over the resting period between the first and second seasons. Familiar illustrations are turnips, parsnips, carrots, beets, and radishes. Most of these cultivated forms have been developed by breeding and selection from wild plants having the capacity so to develop,

FIG. 225.—Portion of a frond of the fern, *Tectoria cicutaria*, showing young plantlets developing from bulbils on the leaf. (Cf. Fig. 387.)

but failing more or less to do so in the wild state, unaided by the gardener.

The poppy anemone (*Anemone coronaria*), though setting no seeds in France, is widely distributed in the fields in the central part of that country; this is brought about exclusively by its propagation by tuberous roots.[1]

[1] According to Alphonse de Candolle (*fide* G. Thuret). Annuaire du Conservatoire et du Jardin Botaniques de Geneve **2**: 36. 1898.

k. By Leaves.—A familiar example of natural vegetative propagation by leaves is found in *Bryophyllum crenatum*, of our greenhouses. In the notches of the leaf margins of the foliage of this plant young plantlets develop, often in great abundance. In time the plantlets or the leaves fall off and the plantlets take root in the soil, thus giving rise to new plants (Fig. 220). Other plants that propagate in this way are the sundew (*Drosera rotundifolia*, Fig. 223), the walking fern (*Camptosorus rhizophyllus*, Fig. 224), and other ferns such as the bladder fern (*Cystopteris bulbifera*), native in the Northern States and Canada, *Woodwardia orientalis* and *Tectoria cicutaria*, the last two found, in the United States, only in greenhouses (Figs. 225, 387). The tropical waterlily, *Nymphaea micrantha*, also freely reproduces by the formation of small plantlets at the tips of the leaf-stalks (Fig. 226).

FIG. 226.—Portion of a plant of the waterlily, *Nymphaea micrantha*, showing young plantlets that have developed at the end of the petiole. The larger flowers belong to the parent plant, the smaller flowers to the plantlets. This species is also known horticulturally as *Nymphaea Daubeniana*.

CHAPTER XVI

HOW SEEDS ARE MADE

The observation of animals and the study of plant physiology might lead one to infer that the main object in life of living things is to feed and grow. Many pages in this book are devoted to describing how the plant absorbs water and food elements from soil and air, and how it grows. Root, stem, leaves, green color, and the various tropistic adjustments to water, light, gravity, and other factors of environment all minister to the "selfish" (*i.e.*, individual) needs of the plant—to feeding and growing. But it is only superficial observation and thought that would lead one finally to the conclusion that a plant's chief "aim" in life is to feed and grow.

FIG. 227.—Inflorescence of an orchid (*Habenaria lacera*), showing bracts along the peduncle (at the left), and bractlets at the base of each pedicle, and also between the flowers and the bracts.

Nor must we confuse our own aims in growing plants with the plant's own object in life. We may grow plants for their flowers, their fruits, their beautiful foliage, their effect in the landscape, or their products—such as lumber, turpentine, drugs, perfumes, and other products; but *the chief end of every plant is to produce seed,* or its equivalent; everything else that a plant does is to ensure that result. In other words, while the plant may appear to be functioning for itself it is, in reality, functioning for others—for the race to which it belongs.

And the bearing of fruit and seed is exhausting to the plant. *Annuals* bear seed once, at the end of their first season, and then die—root, stem, and leaf. *Biennials* take their entire first year to manufacture and store up food for the blossoms, fruit, and seed formed the second year, and die at the end

FIG. 228.—At the left, the globeflower (*Trollius laxus*), showing 5 petal-like hypsophylls ("sepals"), and one dissected leafy bract on the peduncle below the flower. The petals of this flower are very small (shorter than the stamens) and do not show in the illustration (Cf. Fig. 244). In the middle, the European Globeflower (*Trollius Europaeus*), showing a gradual transition from a green, dissected, leaf-like bract (close up under the flower at the right) to yellowish, notched bracts with green tips, then yellow, entire-, but green-tipped bracts, and finally the yellow, entire-tipped and petal-like bracts. At the right an inflorescence of a Dandelion (*Taraxacum*) to show the *involucre*—a double one, consisting of two or more outer whorls of reflexed bracts, and a single, inner whorl of longer, erect bracts.

of the second season. *Perennials* continue to live, flower, and bear fruit year after year for more than two years. An extreme case is the California Bigtree (*Sequoia gigantea*) which may live for two thousand years or more, shedding only dead leaves from time to time but, like most conifers, remaining evergreen because there

are always some green leaves on the branches. In the temperate zone deciduous trees and shrubs shed their leaves at regular annual intervals, with the approaching drought of winter; while, in the tropics, broad-leaved deciduous trees may be shedding old leaves and producing new leaves at the same time throughout the year. The Live Oak (*Quercus virginiana* Miller), various species of Holly (*Ilex*), *Leucothoe*, *Yucca*, *Aucuba japonica*, the English or Cherry Laurel (*Prunus Laurocerasus*), the Bearberry (*Arctostaphylos*), and numerous others illustrate the broad leaved evergreens. In plants of this type the main plant-body persists from year to year, but the modified flowering branches (the inflorescences) die after flowering and fruiting.

Some perennials have perennial roots or perennial rhizomes only, such as Quick Grass, Solomon's Seal, Trillium, and others, in which the entire shoot above ground dies down annually after flowering. The Houseleek (*Sempervivum*) is perennial by offsets which may live for several years, but always die after flowering. One of the most noted examples is the Century Plant (*Agave* sp.), which may live for decades, but always dies after flowering once, apparently being exhausted by the production of its enormous flowering stalk.

Blossoming and fruit-bearing are thus seen to be more or less exhausting to a plant, and certain practices of the experienced gardener are adopted in recognition of this fact. Thus, for example, a wise gardener will pick off all the flower buds, or at least all the blossoms, from his rhododendrons the first year after they are set out, not allowing them to bloom until they have fully recovered from the shock of transplanting, and have become adjusted to their new surroundings. For a similar reason a good orchardist will remove a large percentage of the blossoms from his apple trees, or from his grape vines, thus insuring not only larger (though fewer) fruits, but also reducing the annual drain on the plant. This practice is resorted to in the production of the remarkably large bunches of hothouse grapes.

In the preceding chapter we noted two main types of reproduction: one involving cell-divisions only; the other involving cell-fusion. It was also noted that cell-fusion is a step in sexual reproduction. In seed-bearing plants the structure involved in this function is the flower.

The Meaning of Flowers.—While stems, roots, and leaves may, at times, serve the purpose of vegetative propagation, their essential and primary purpose, as noted above, is the nutrition of the individual plant. They all make demands upon the plant as a whole, but in turn they all contribute something to its nutrition; they are mutually interdependent. With the flower, however, it is quite different. Here is an organ that makes large demands upon the plant as a whole but, with few exceptions, contributes little or nothing to the nutrition or other needs of the individual that bears it, but only to the production of off-

FIG. 229.—Inflorescences of the Flowering Dogwood (*Cornus florida*). Each inflorescence is composed of numerous, inconspicuous flowers surrounded by an involucre of four white or pinkish, petal-like bracts.

spring of that individual. It is essentially an organ for reproduction, and specifically for the formation of seeds.

We shall first consider briefly the arrangement of flowers on the plant and then the structure and function of individual flowers and their parts.

Definitions.—The manner of arrangement of flowers on the flower-stalk, was called by Linnaeus the *inflorescence.* It is now common to refer to the flower-cluster as "the inflorescence."

Like the flower itself, the inflorescence is a modified branch, or portion of a branch. The main stem or axis of an inflorescence is the *peduncle,* while the stems of the individual flowers are called *pedicels.* When the inflorescence consists of a single

flower the flower-stalk is also called a peduncle. The more or less reduced, or otherwise modified leaves borne on or near the inflorescence are termed *hypsophylls* or *bracts* (Fig. 227). A leaf that *subtends* an inflorescence, that is, that bears an inflorescence in its axil, is also a bract. A bract borne on or subtending a pedicel is a *bractlet* or *bracteole* (*e.g.*, Lily-of-the-valley, Fig. 231, *a*) *Cf*, also, Fig. 466.

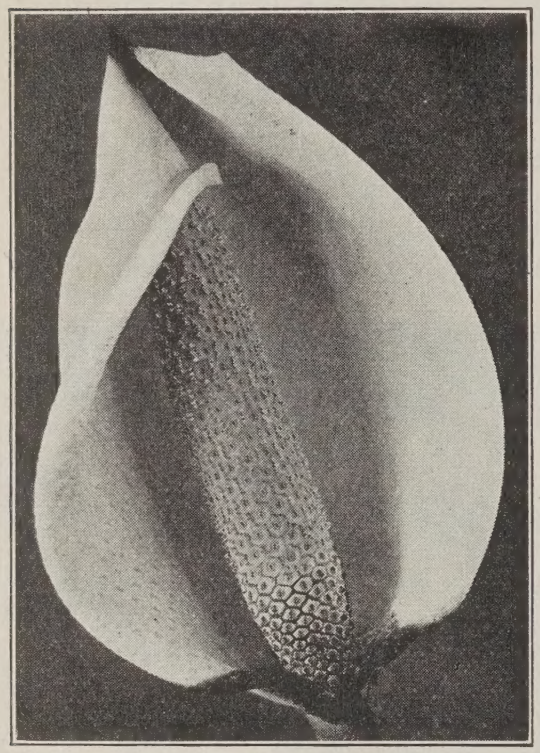


Fig. 230.—Inflorescence of *Monstera deliciosa*. The conspicuous, white spathe surrounds the spadix which bears the flowers, the latter without floral envelopes. The hexagonal areas are the tops of the ovaries, the shape being due to the crowding. The black dots are the stigmas at the top of the short styles. Each ovary is surrounded by four stamens, but these do not show on the older flowers at the lower part of the spadix. The ovaries, when ripe, make *delicious* eating, whence the name. They have a mixed flavor of pineapple and banana. Before they are thoroughly ripe the tissues of the ovaries are full of needle-shaped crystals of calcium oxalate, which are very painful in the mouth and throat.

Every flower, like every other branch, is born in the axil of a leaf or bract (see p. 266), but in some species the bract is very minute, in others (some of the Mustard Family, or Cruciferae) *obsolete*, that is, not evident, being vestigial or rudimentary. In some species it falls away very early (*fugacious*).

A circle or spiral of bracts is an *involucre*, and may be associated with a flower cluster (*e.g.*, dandelion, coltsfoot), or with a single flower, as in *Hepatica*, Winter Aconite (*Eranthis*), Globeflower (*Trollius*), and others (Fig. 228).

In many plants the transition from foliage leaf to bract or hypsophyll is very gradual, proceeding from the lower part of the stem toward the apex; at intermediate points it is quite arbitrary whether one calls a structure a leaf or a bract, but usually the foliar organs near to or subtending a flower are called bracts because of their position, although they may closely resemble the foliage leaves.[1]

[1] The terms hypsophyll and kataphyll were introduced by K. F. Schimper (1803–1867). The term *hypsophyll*, as the etymology indicates, refers to

In certain species the bracts are large and conspicuous, in fact being often mistaken for petals, as in the dogwoods (*Cornus florida*, and *Cornus canadensis*, Fig. 229); or the bright red bracts of *Poinsettia*.

In such an inflorescence as the Jack-in-the-Pulpit, Calla Lily, Tail-flower (*Anthurium*), and other plants of the Arum Family, the bract is the most conspicuous and showy part of the inflorescence, the individual flowers being quite inconspicuous and borne sessile on a fleshy axis, the *spadix* (Fig. 230). Such a bract is called a *spathe*.

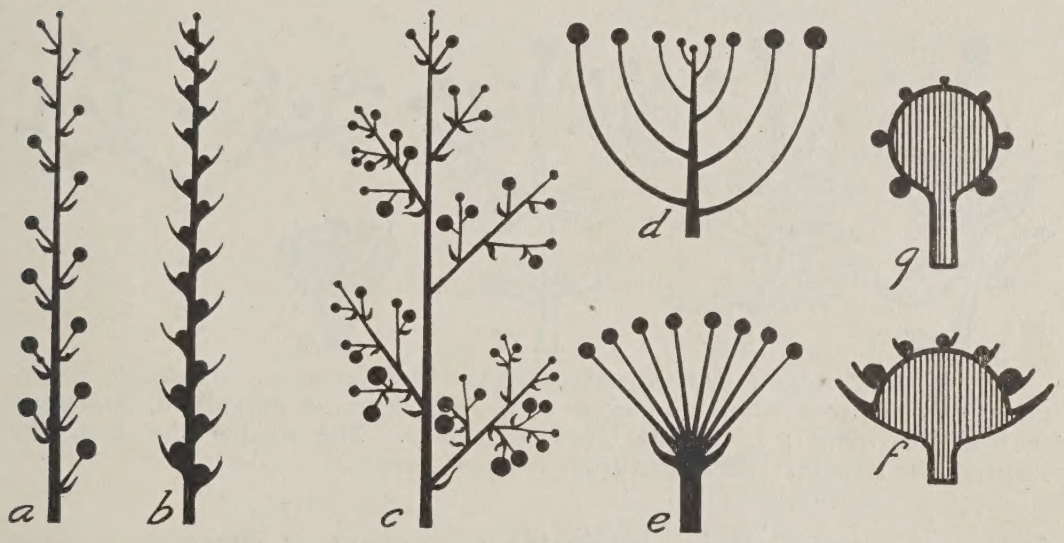


FIG. 231.—Types of racemose or centripetal inflorescence. *a*, simple raceme; *b*, spike; *c*, panicle; *d*, corymb; *e*, umbel; *f*, head of Compositae type; *g*, head of clover type. The smaller the dots, the younger the flowers. (Redrawn from various sources.)

The bracts of the individual florets of the *head* of the Compositae are called *palets* or *chaff*. The latter term is more familiar as applied to the *glumes*, or chaff-like bracts of the inflorescence of cereals and other grasses (Fig. 567).

---

foliar organs (not strictly foliage leaves) on the *upper* part of the branch (*e.g.*, involucre), while *kataphyll* is used to designate foliar organs at the *lower* part of the branch, such, for example as bud-scales, which are at the very base of each season's growth of a branch. As Goebel states (*Organography* **2**: 390), these are very convenient terms; they merit a more general use than has obtained in the United States.

When the peduncle arises from the ground, as in the onion, dandelion, violet, primula, tulip, and numerous other plants, it is termed a *scape*.

Types of Inflorescence.—Every individual flower is *terminal*, that is, borne at the end of its own stalk, but all flower clusters fall into either of two groups—one having a flower terminal on the peduncle; the other having all the flowers borne by lateral peduncles. In the latter case the growth is *indeterminate*, and the formation and opening of flower buds continues until internal exhaustion or external conditions bring the process to an end. Obviously the opening of the flowers then proceeds from circum-

FIG. 232.—Types of cymose or centrifugal inflorescence. *a*, simple determinate; *b*, cyme; *c*, compound cyme (*e.g.*, hydrangea, dogwood); *d*, glomerule (a head-like cyme); *e*, fascicle (crowded cyme). The smaller the dots, the younger the flowers. (Redrawn from various sources.)

ference to center; it is *centripetal*, ascending or *racemose*. This becomes evident by prolonging the pedicels, in imagination, until they are of uniform length (Fig. 231).

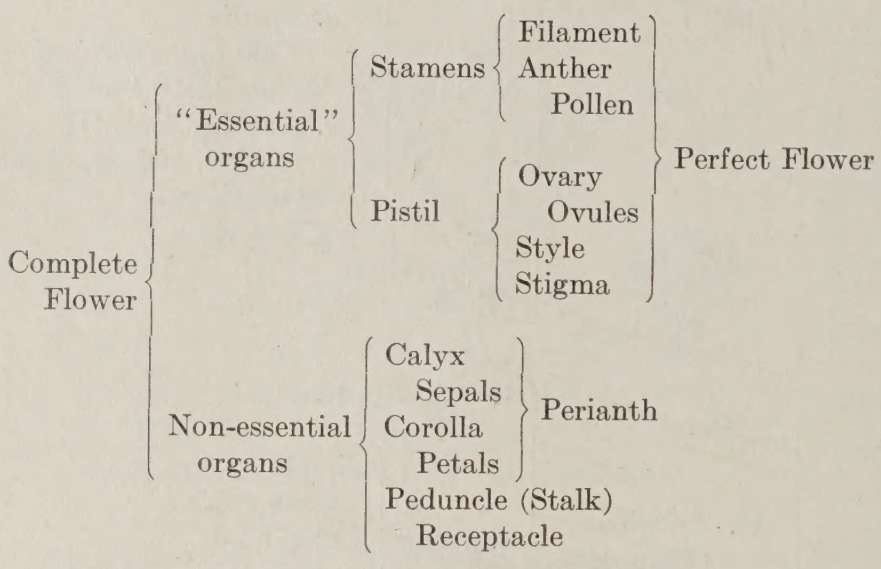
When the main axis terminates in a flower bud, that bud is the first to open. The inflorescence is then *determinate*, and the opening of buds proceeds from center to circumference, *i.e.*, is *centrifugal*, descending or *cymose* (Fig. 232). When there is only one flower the inflorescence is *simple*.

No attempt will be made here to define the various types of flower cluster comprised in the above two classes, but a study of the illustrations referred to, and of the following table, giving the names of the various types, especially when supplemented by a laboratory or field study of actual specimens, should enable the student to frame his own definitions.

- Inflorescence
  - I. Axillary, (Indeterminate, centripetal)
    - 1. Raceme
      Lily-of-the-valley, currant
    - 2. Corymb
      Candytuft
    - 3. Panicle (A branched raceme or corymb
      Oat, Virginia creeper
    - 4. Umbel
      - Simple
        Onion, milkweed
      - Compound
        Parsnip, carrot, parsley
    - 5. Head
      Clover, lettuce, dandelion, marigold
    - 6. Spike
      - Simple
        mullein, plantain
      - *a.* Spadix
        Cala lily, Jack-in-the-Pulpit, Anthurium
      - *b.* Catkin (Ament)
        Willow, hickory, chestnut
      - Compound
        Wheat, rye
    - 7. Syconium
      Fig
  - II. Terminal, (Determinate, centrifugal)
    - 1. Solitary, terminal
      Poppy
    - 2. Cyme
      - Simple
        Crab apple
      - Compound
        Mountain Ash, elder, Viburnum
    - 3. Glomerule
      Dogwood, box, nettle
    - 4. Fascicle
      Sweet William
  - III. Mixed
    - 1. Thyrsus
      Lilac, horsechestnut, privet
    - 2. Mixed panicle
      Fire pink (Silene virginica)
    - 3. Verticillaster
      Catnip, peppermint

The Parts of a Flower.—The parts of a flower, now familiar to nearly everyone through lessons in nature study in the lower grades, have been briefly reviewed in Chapter I (p. 7). The

parts are arranged in circles or *whorls*, and the number of whorls and the number of parts in a given whorl may vary from *none* to *numerous*. Moreover the arrangement or insertion of the whorls with reference to each other may vary, and the parts have an infinite variety of shapes, often being disguised almost beyond recognition. There is, therefore, no really "typical" flower, although any given flower may be arbitrarily chosen as a type with which to compare the others; or a simple, *generalized* flower may be constructed in imagination out of the structural elements met with in various flowers. A *complete flower* has the following parts.



A flower that has both stamens and pistil is called *perfect* because, in these organs, it has everything necessary to make seeds, for sepals and petals are not absolutely necessary for that. A flower that lacks any of the four whorls is *incomplete*, but is not *imperfect* unless it lacks either stamens or pistil. When a flower lacks one of the whorls of the perianth it is usually considered that the corolla is lacking, and the flower is called *apetalous*. These four main types of flowers, *complete, perfect, staminate, pistillate*, are illustrated in figures 230, 404, 405, 534, 537, and 538.

A perfect flower is sometimes called *hermaphrodite*. When *staminate* and *pistillate* flowers occur on the same plant, the plant is *monoecious* (of one household Fig. 233); when they occur on

separate plants the plants are *dioecious* (of two households, Fig. 234).

The Pistil.—In order to understand how seeds are made we must first understand the finer structure, or *anatomy* of the essential floral organs. The pistil, when present, is always terminal, or at the apex of the floral axis; the other floral organs are lateral members. A median longitudinal section of a generalized pistil passes from tip to base, through *stigma*, *style*, and *ovary* (Fig. 235).

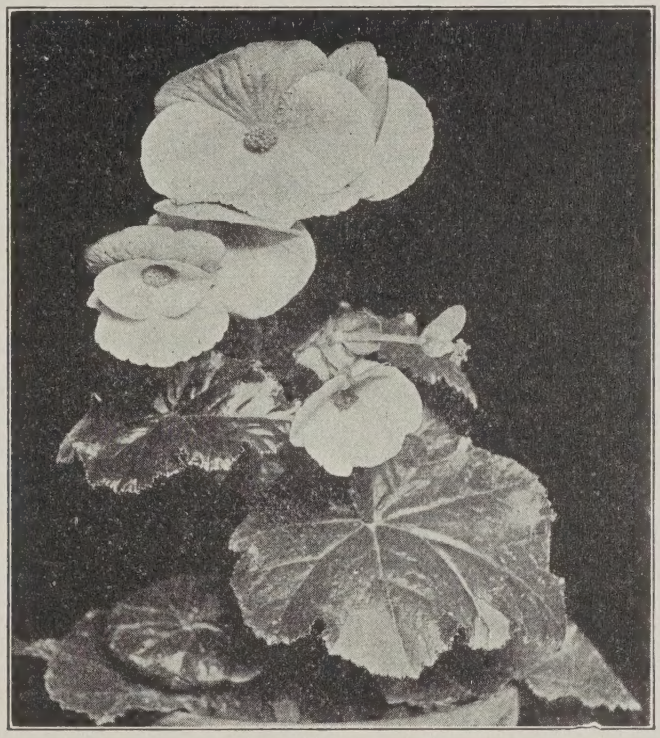


FIG. 233.—Monoecious, imperfect flowers of a rex begonia; staminate above; pistillate below; one of the latter with the perianth removed to show the ovary and stigmas. (Photo by Elsie M. Kittredge.)

The *stigma* is essentially the surface on which the pollen-grains germinate. It may be at the tip of the style, or lateral, extending down the side. It may be simple or compound (*i.e.*, lobed), and may possess a variety of shapes, and various kinds of surface, such as smooth, sticky, feathery, etc. All these variations indicate the different ways in which plants have solved the problem of insuring the adhesion and germination of pollen grains.

The pistil may or may not have a well defined *style*, and the style may or may not be hollow. It is commonly terminal,

(*i.e.*, arising at the apex of the ovary), but may be lateral (Strawberry), or it may arise near the base of the ovary, as in *Alchemilla.* It may *persist* in the fruit (Pea,) or it may be deciduous (Snapdragon). It has a variety of forms in different species, *e.g.*, club-shaped (Lemon), thread-like or filiform (*Fuchsia*), or petal-like (*Iris*).

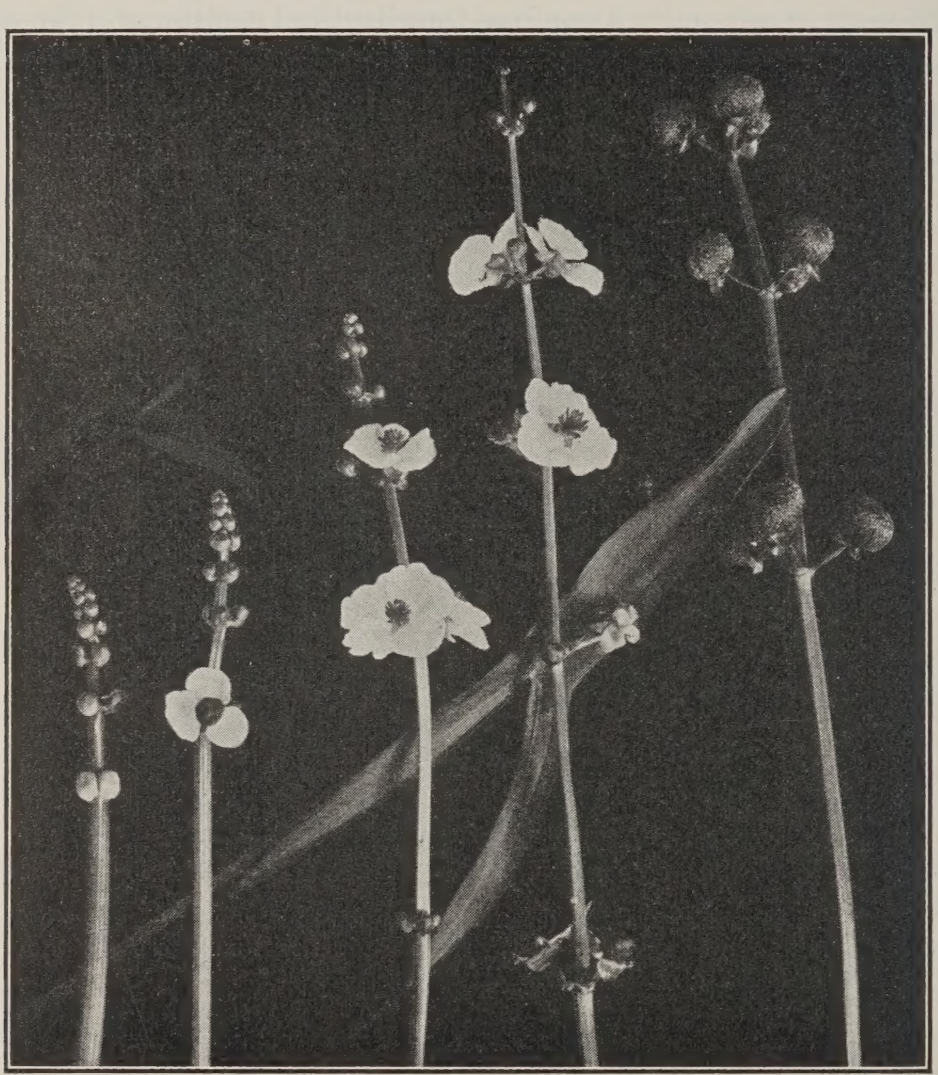


FIG. 234.—Dioecious, imperfect flowers of Arrowhead (*Sagittaria*). At the left, branches with staminate flowers only; in the middle, branches with pistillate flowers only; at the right, pistillate branch, bearing fruit.

The *ovary* is the basal part of the pistil and contains the *ovule* or ovules. A simple pistil, such as that just described, is often called a *carpel.* A *compound pistil* is composed of several carpels more or less closely united into one structure (Fig. 236). In the latter case two or more styles may arise from the one com-

pound or *syncarpous* pistil. Many flowers, such, for example, as the Buttercup and Strawberry (Fig. 426), possess several simple pistils. The pistillate part of a flower, whether of one simple pistil, a compound pistil, or of several pistils, is called the *gynoecium*. The ovary and stigma are essential parts of a pistil; the style may or may not be wanting.

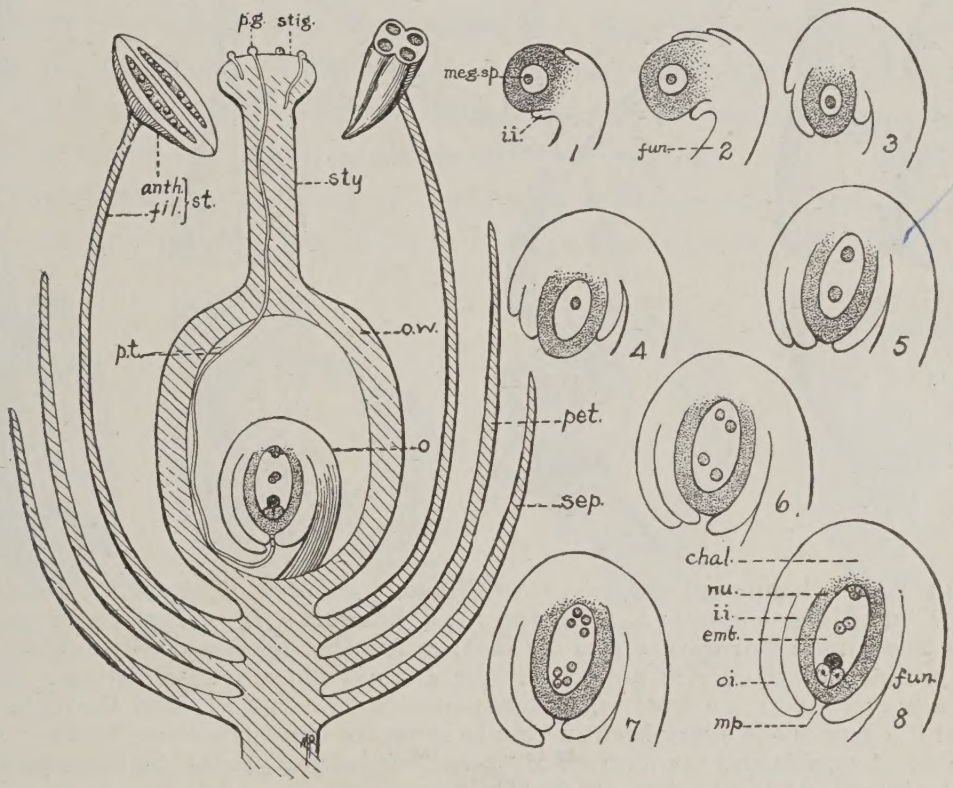


FIG. 235.—At the left, diagram of the anatomy of an angiospermous flower shortly after pollination; *anth*, anther; *fil.*, filament; *st.*, stamen; *stig.*, stigma; *p.g.*, pollen grains germinating; *sty*, style; *pt.*, pollen tube; *o.w.*, ovary wall; *o.*, ovule, containing embryo-sac; *pet.*, petal; *sep.*, sepal. 1–8, Stages in the development of the female gametophyte (embryo-sac); *meg. sp.*, megaspore-mother-cell; *i.i.*, inner integument; *o.i.*, outer integument; *fun.*, funiculus; *chal*, chalaza; *nu.*, nucellus (megasporangium); *emb.*, embryo-sac. All diagrammatic.

The *ovules* are born within the ovary,[1] being attached either at the base (*erect*), as in the Buckwheat (Figs. 238 and 239); or on the central axis where the carpels of a compound pistil unite, forming two or more compartments or "cells" (Apple and Tomato, Fig. 431); or on the wall, as in the Bean and Cucumber. The surface or place to which the ovules are attached is called the

[1] It has been suggested that, since it contains ovules, a more appropriate term for the ovary would be *ovulary*.

placenta; this may be either *basal*, *central*, or *parietal*, according to the arrangement of the ovules, as noted in the preceding

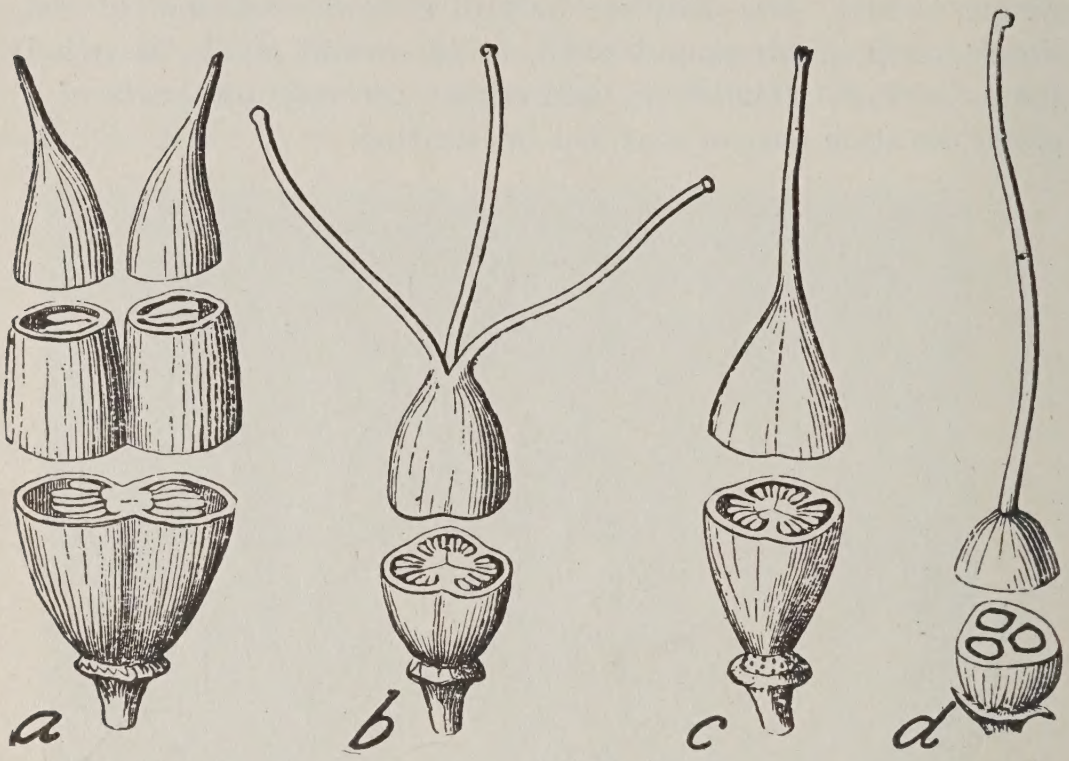


Fig. 236.—Compound pistils. *a*, Saxifrage, composed of two carpels united below but distinct above; *b*, Common St. Johnswort (*Hypericum perforatum*), with three united ovaries, styles distinct; *c*, Another species of St. Johnswort (*H. prolificum*), the styles united but the stigmas more or less distinct. The styles may split in the fruit; *d*, Tradescantia, with carpels united throughout. In all the figures the ovary is cut across to show the correspondence between the number of carpels and the number of "cells" of the ovary; also the placentation or attachment of the ovules. (After Gray.)

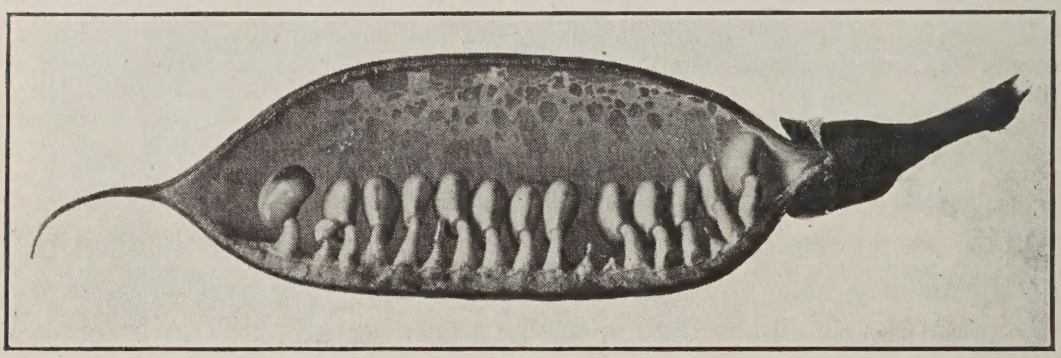


Fig. 237.—Blue False Indigo (*Baptisia australis*). One half of a seed-pod (legume), showing placentation. Each ovule is attached to the placenta by a thick fleshy funiculus. One-half of the placenta and half of the ovules belong to the valve that shows; the other halves to the valve that was largely cut away.

sentence. Each ovule is attached to the placenta by a stalk called the *funiculus* (Fig. 237).

The ovule is the structure that develops into a seed. It may be straight (*orthotropous*), or curved. In the latter case it may be *campylotropous*, *amphitropous*, or *anatropous* (Figs. 238 and 239).

An orthotropous ovule finds a typical illustration in the Buckwheat (Fig. 239). In longitudinal section one sees the stalk or funiculus, and two "seed-coats" or *integuments*, an outer and an inner. At the end opposite the stalk is the tiny opening (*micropyle*) where the seed coats do not quite come together. The main portion of the ovule, surrounded by the integuments, is the *nucellus*, and within the nucellus is the structure (*embryo-sac*) in which the future embryo will develop.

The *mature embryo-sac* is a complex cellular structure enclosed by a common *wall* (Fig. 240). Within the wall, at the basal end,

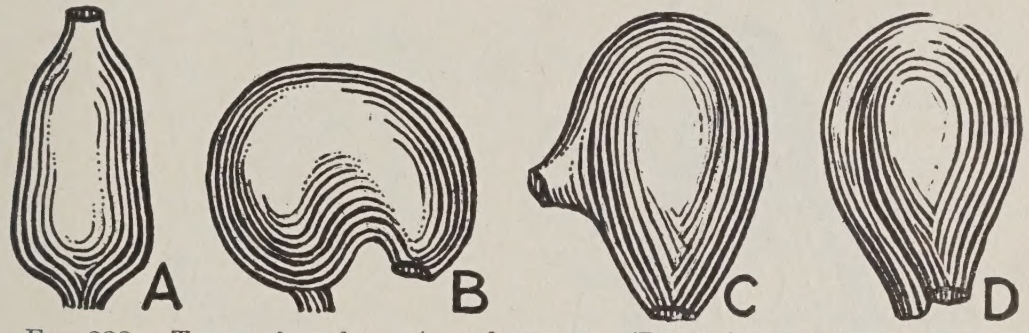


FIG. 238.—Types of ovules. A, orthotropous (Buckwheat); B, campytropous (Chickweed); C, amphitropous (Mallow). D, anatropous (Violet). (Redrawn from Gray.)

are several cells (commonly three) called the *antipodal* cells. At the opposite end, next to the micropyle, are three more cells, one of which is larger than the others and richer in protoplasm; this is the *egg-cell*, or egg. The other two cells are called *synergids*, or helpers. Near the center of the embryo-sac are, at first, two nuclei, which later fuse, forming the *fusion-nucleus* or *primary endosperm-nucleus*. The cavity also contains more or less cytoplasm, which becomes organized about the various nuclei to form the seven or eight cells.

By referring to page 9 it will be seen that many of the terms used in describing the ovule are (naturally) the same as those used in describing the seed, which is only a ripened or matured ovule.

The Stamens.—The floral organs immediately surrounding the pistil or gynoecium are the *stamens*. As noted on page 7, each

stamen comprises a stalk or filament, bearing at its tip an *anther*. Within the anthers are *pollen-grains* (Figs. 235, 246). Every young pollen-grain is at first a single cell (with one nucleus), and is, in reality, a microspore (p. 421), but mature pollen-

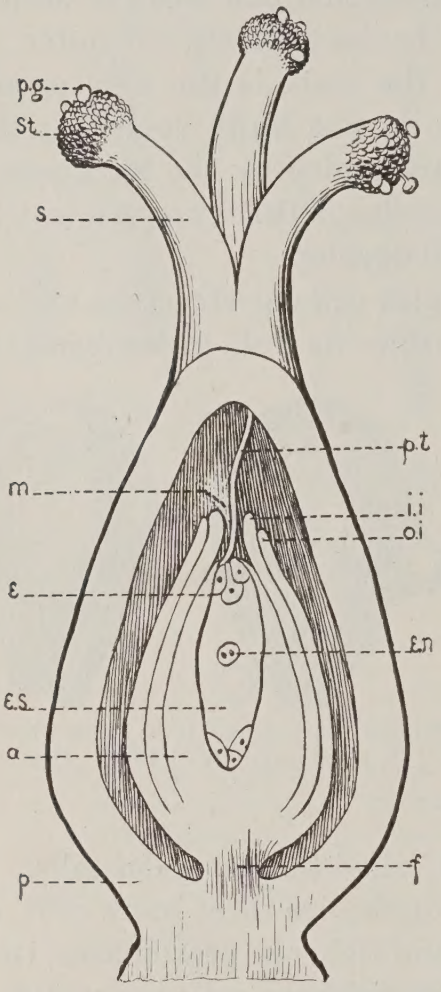


Fig. 239.

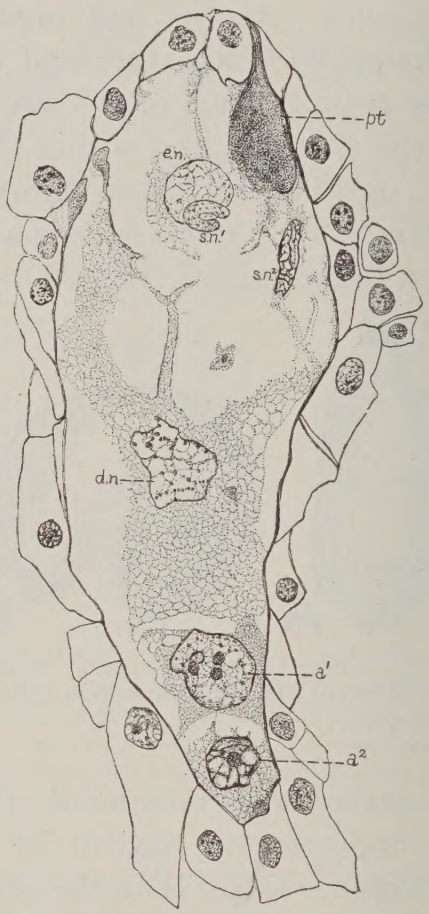


Fig. 240.

Fig. 239.—Diagram showing structure of pistil and orthotropous ovule of Buckwheat (*Fagopyrum*) in longitudinal section, greatly enlarged. Stigmas with pollen-grains adhering. One pollen tube has entered the micropyle (*m*) at the tip of the ovule. *es*, embryo-sac; *e*, egg-cell. (Modified from Gray.)

Fig. 240.—*Lilium canadense*. Embryo-sac at the time of fertilization; a^1, a^2, antipodal cells; *dn.*, primary endosperm-nucleus; *pt.*, remains of pollen tube; *e.n.*, egg-nucleus; $s.n.^1$, sperm-nucleus, fusing with the egg-nucleus; $s.n.^2$, second sperm-nucleus, which may later fuse with the primary endosperm-nucleus, thereby accomplishing *double fertilization*. (Redrawn from camera lucida drawing by O. E. White.)

grains commonly have two or three nuclei (Fig. 241). When there are two nuclei one is the *tube-nucleus*, the other the *generative nucleus*, the two being formed by the division of the nucleus

of the young pollen grain. By the division of the generative nucleus two *sperm nuclei* result.

The Floral Envelope.—The floral envelope or *perianth* has also been briefly described (p. 7), with its two circles or cycles—the outer one being the calyx, with its sepals (separate or more or less united), and the next inner one the corolla, with its petals, also either separate or more or less united. The floral envelope presents itself in an almost endless variety of variations as to size, form, and color. The variations in shape (morphological variations) of these organs will be noted in connection with the descriptions of the various groups of plants (pp. 571, *et seq.*).

The derivation of the parts of the perianth forms an interesting and sometimes difficult study. In so-called "single" flowers,

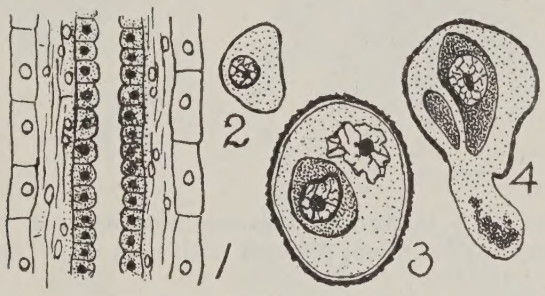


FIG. 241.—Dog's-tooth Violet (*Erythronium*). 1, longitudinal section of hollow style, showing glandular cells of the conducting tissue that lines the stylar tube; 2, young pollen-grain (microspore); 3, pollen-grain (male gametophyte), showing two nuclei (generative nucleus and tube nucleus) derived by the division of the microspore nucleus; 4, pollen-grain germinating. 1 and 4 are from *E. albidum;* 2 and 3 from *E. americanum.* (After J. H. Schaffner.)

having a simple (*i.e.*, not doubled) corolla, and a calyx, the parts of the corolla (petals) are usually derived by a transformation of the *primordia* (initial stages) of stamens. In double flowers the additional petals may represent additional "transformed" stamens (*petalody of the stamens*) or "transformed" carpels (*petalody of the carpels*). In flowers having a perianth of only one whorl of parts this whorl is considered a calyx, the corolla being considered as wanting. The parts of the calyx may be derived in one of two ways: either by transformation of the primordia of stamens, as for example in Buttercup (*Ranunculus*), *Anemone*, and Rose (Figs. 242, 243, 429), or by transformation of the primordia of hyposphylls. The latter is the origin of the petal-like perianth of the Globeflower, *Trollius* (Figs. 228, 244). In the latter flower the petals are inconspicuous organs, shorter than the

stamens, and serving chiefly to bear nectaries near their bases. In some apetalous flowers (such, for example, as, *Hepatica*) the

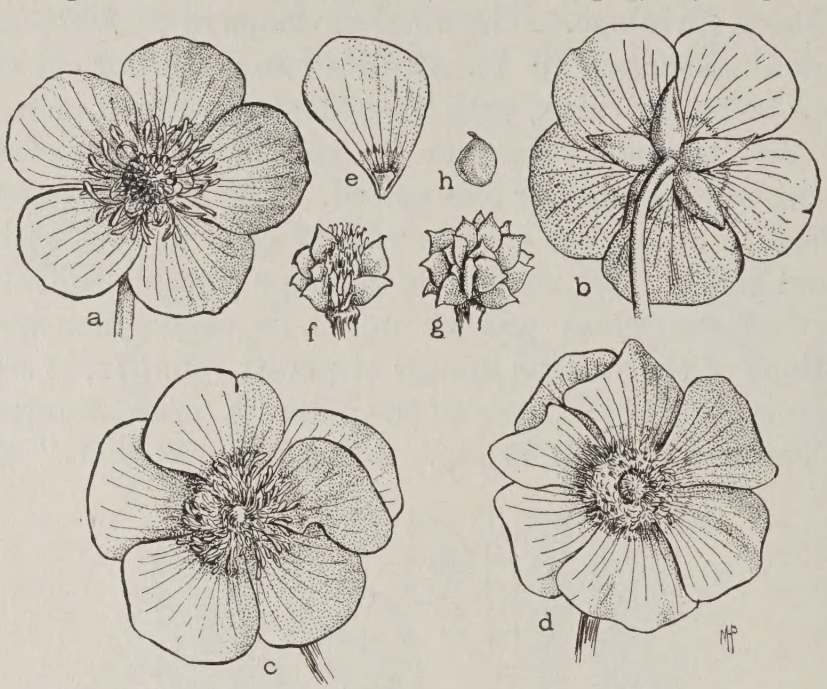


FIG. 242.—Flower of a buttercup (*Ranunculus* sp.); *a*, *b*, normal, showing 5 petals; *c*, *d*, petalody of stamens; *e*, petal with nectary at its base; *f–h*, ripened ovaries. (*Cf.* Figs. 243, 429.)

FIG. 243.—Rue anemone (*Anemonella thalictroides*). 1, normal flower with 5 petals; 3, petalody of stamens; 4, coalescence of petals (c^1); 2, coalescence (c), and petalody of stamens. At 2*s* is shown a stamen partially transformed into a petal, but with a portion of the anther still remaining. (*Cf.* Figs. 242, 429.)

number of parts of the calyx varies from flower to flower. In the case of *Hepatica* those above the normal number are derived from

the primordia of stamens, the others being hypsophylls. In all such cases it is not uncommon to say that the stamens have been "transformed" into sepals (or petals, as the case may be). This,

FIG. 244.—*Trollius laxus.* Flower with two so-called "petals" (transformed hypsophylls) removed so as to disclose the inconspicuous true petals, shorter than the stamens, and serving chiefly to bear nectaries. The flower-stalk bears a leaf-life bract. (Cf. Fig. 228.)

however, is not correct, for that which appears as a sepal or petal has never been a stamen. It is better to say that a stamen has been replaced by a sepal or a petal.[1]

[1] Cf. Goebel, *organography*, **1**:180; **2**:548–551.

Arrangement of Whorls.—In the ground plan of the flower the order of parts is as follows, beginning with the pistil or pistils (*gynoecium*) at the center; stamens (*androecium*), petals (*corolla*), sepals (*calyx*). As viewed in longitudinal section there are three main types, as follows (Cf. Fig. 245):

1. *Hypogynous.*—The perianth and stamens are inserted on the receptacle outside of and *below* the pistils, and quite free from them. The flower is then said to have a *superior* ovary (*e.g.*, magnolia, buttercup, lily, primrose, plum, etc.).

2. *Perigynous.*—The pistil is free in a more or less cup-shaped receptacle, on the edge of which are borne the perianth and the

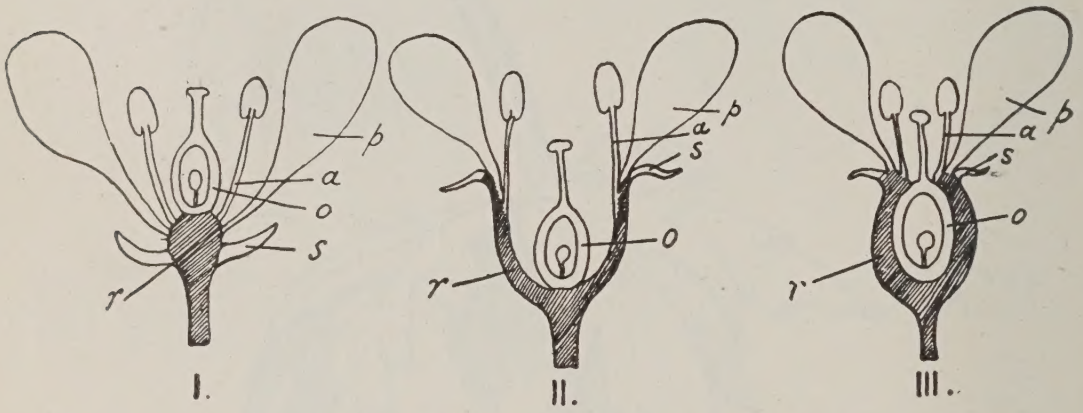


FIG. 245.—Diagrams of longitudinal sections through, I, a hypogynous flower; II, a perigynous flower; III, an epigynous flower. *r*, receptacle; *s*, sepal; *p*, petal; *a*, stamen; *o*, ovary of the pistil. (After Percival.)

stamens, *around* (*peri-*) the pistils, as in cherry; or the calyx may be adnate to the lower part of the ovary (as in the Purslane); or, again, the calyx may be adnate clear to the top of the ovary and the stamens and petals inserted on the calyx (as in hawthorn).

3. *Epigynous.*—The perianth and stamens are inserted on the edge of a hollow receptacle which grows up closely around the ovary, leaving only the styles and stigmas free. The perianth and stamens *appear* to be inserted on the ovary, hence the term *epigynous*, meaning "on the gynoecium." The flower is said to have an *inferior* ovary (*e.g.*, apple, pear, squash and other members of the Gourd Family, dandelion and other members of the Composite Family, etc.).

How the Seed Is Made.—For our purpose the main object in knowing the parts of the flower is so that we may understand the processes by which a seed is made.[1] The steps in this process are as follows:

A pollen grain from the anther is deposited on the stigma. This is called *pollination.*

After pollination the pollen-grain sends out a slender threadlike growth —the *pollen-tube.* This process is the *germination* of the pollen-grain (Fig. 246), and is favored or induced by the condition of the stigma and the atmosphere as to moisture, and also by nutrient materials secreted by the stigma. The pollen-tube grows down the style, either making its way through the *conducting tissue* of the style or often, when the style is hollow, through the *stylar canal* (Figs. 241, 246). When the style is hollow the conducting tissue is confined to the walls. It serves to nourish the growing pollen-tube, and it is an expansion of this tissue at the tip of the style that forms the stigmatic surface. This tissue extends without interruption from the stigma down through the style to the ovules.

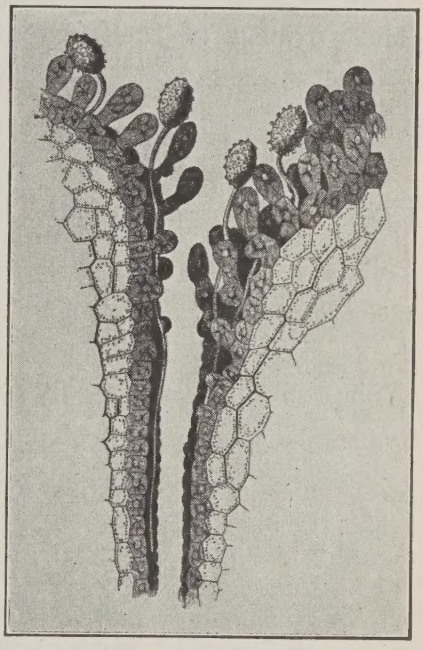


FIG. 246.—*Lilium Martagon.* Longitudinal section of the stigma and upper part of the style. The pollen-grains, caught on the papillae of the stigma, have germinated, and the pollen-tubes are growing down along the walls of the style-canal, nourished by the specialized cells that line it. (After Dodel-Port.)

During the germination of the pollen and the growth of the pollen-tube the two sperm-nuclei are formed (if this has not already occurred) by the division of the generative nucleus, and these and the tube nucleus pass down the elongating pollen-tube.

[1] Another need for knowing floral structure is in connection with the *determination* of the plant—that is, ascertaining its position in the classification of plants, and thereby its name, if it has one. The great French biologist, Lamarck, in his *Zoological Philosophy* (Chapter II), was one of the first to point out that the chief affinities among animals are based on the non-reproductive organs but, among plants, on the parts essential to reproduction.

The pollen-tube continues to grow until it reaches the ovary, finds an ovule, and then a micropyle, through which it passes to the embryo-sac.[1] When the tip of the tube has passed through the micropyle to the embryo-sac its wall is ruptured and the sperm-nuclei pass out into the protoplasm of the embryo-sac. One of these nuclei fuses with the egg-nucleus, thus completing the process of *fertilization.* In certain cases the second sperm-

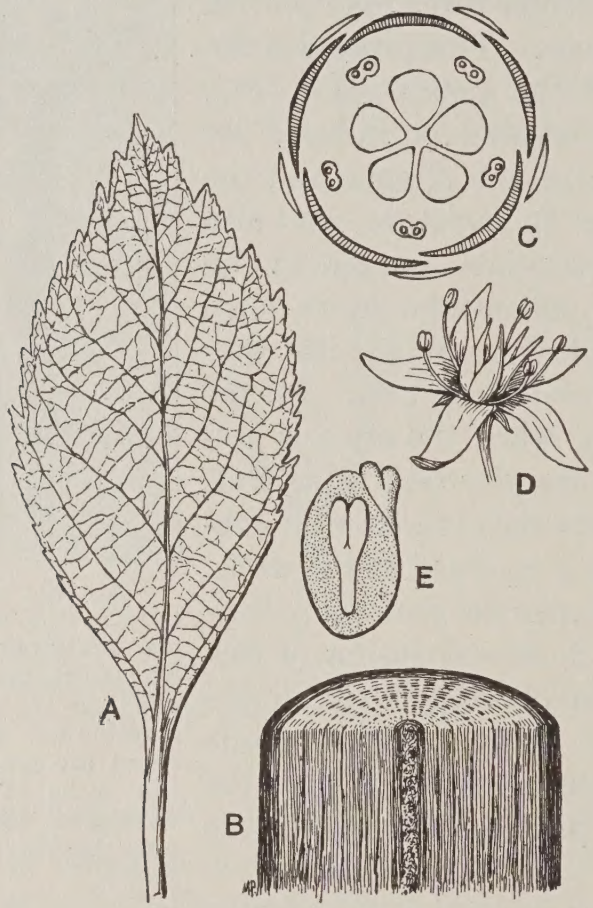


FIG. 247.—Morphology of a typical woody dicotyledonous plant. *A*, leaf, pinnately netted-vein; *B*, portion of stem, showing concentric layers of wood; *C*, ground-plan of flower (the parts in 5's); *D*, perspective of flower; *E*, longitudinal section of seed, showing dicotyledonous embryo and strophiole.

nucleus fuses with the primary endosperm-nucleus, producing *triple fusion,* or *double fertilization* (Fig. 240).

The fertilized egg now begins to develop by a process of successive cell-divisions and growth, and finally becomes differentiated

[1] In certain cases the pollen-tube enters the ovule, not through the micropyle, but through the tissue of the wall of the ovule, often at the *chalaza, i.e.,* where the seed-coats blend. This is called *chalazogamy.*

into an *embryo plant*, with one or more seed-leaves (*cotyledons*), an embryonic stem below the cotyledons and therefore called the *hypocotyl*, and the embryonic bud or *plumule*. All this takes place within the embryo-sac, and at the expense of more or less of the surrounding tissue of embryo-sac and nucellus. If all of this tissue has been absorbed by the growing embryo, the seed

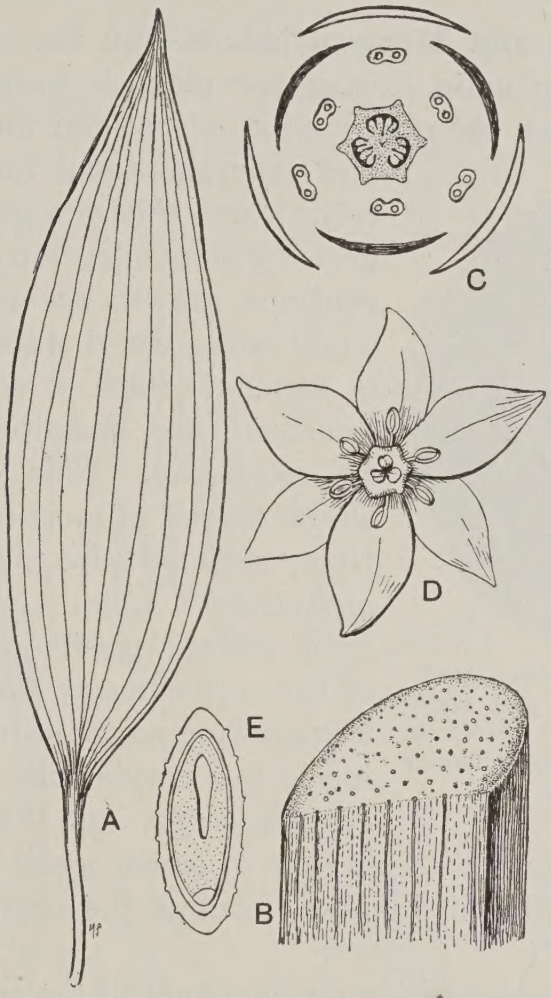


FIG. 248.—Morphology of typical monocotyledonous plant. *A*, leaf, parallel-veined; *B*, portion of stem, showing irregular distribution of vascular bundles; *C*, ground plan of flower (the parts in 3's); *D*, top view of flower; *E*, seed, showing monocotyledonous embryo.

is without nourishment ("albumen") stored around the embryo. In such cases the absorbed nourishment is stored in the embryo, and commonly, as in the bean and most nuts, in the cotyledons; when the tissue of the embryo-sac and nucellus is left around the embryo the seed is commonly called *albuminous* (*e.g.* the castor-oil seed).

If the albumen is derived from the nucellus, as in the Canna, it is called *perisperm;* if it is formed by the division of the (fertilized or unfertilized) endosperm-nucleus within the embryo-sac, as in castor-bean, it is called *endosperm.* The latter is the case in most seeds. In the white pond-lily the albumen is mostly perisperm, though a thin layer of endosperm tissue remains next the embryo.

Dicotyledons and Monocotyledons.—In the development of the embryo the main axis of the plant is formed first. This axis early shows *polarity,* having a root-end and a shoot-end. Near the shoot-end there is formed a *cotyledonary ring,* or zone. When several growing points develop on this ring, and continue growth at approximately an equal rate, a whorl of several cotyledons is formed. Such a seed is *polycotyledonous;* the condition is that of *polycotyledony.* This development is characteristic of most of our coniferous trees, such as pine, hemlock, spruce, and others.

FIG. 249.—John Ray (1628–1705). An early and noted English botanist. First to distinguish monocotyledons from dicotyledons.

In certain plants the development of the cotyledonary ring is confined to two growing points or primordia, resulting in two cotyledons. Such seeds are *dicotyledonous,* and the condition is that of *dicotyledony.* This type of embryogeny is characteristic of an entire group of families, forming the subclass, DICOTYLEDONS (Fig. 247).

In another sub-class the development of the cotyledonary ring is largely or wholly confined to one growing point, resulting in an embryo of only one cotyledon. Such a seed is *monocotyledonous,* and the sub-class the MONOCOTYLEDONS (Fig. 248).

The first botanist who recognized that flowering plants have, as a rule, either one or two cotyledons, was John Ray, who was born in England, November 29, 1627, and died there on January 17, 1705. It was he who introduced the terms monocotyledon and dicotyledon, making the number of cotyledons the basis of

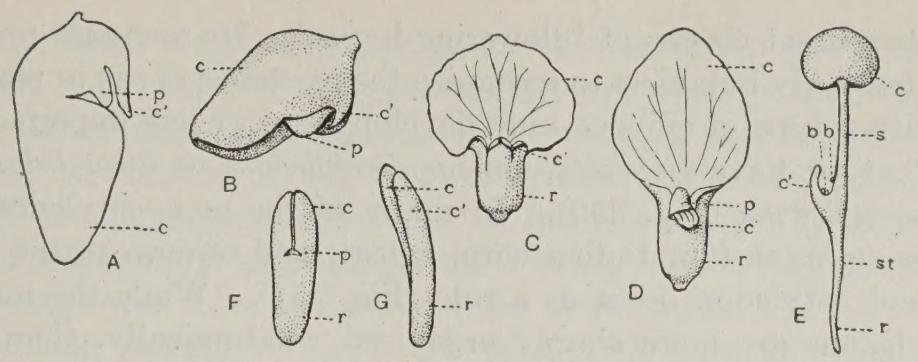


FIG. 250.—A-D, embryos of a "dicotyledonous monocotyledon;" A, *Tamus communis* in longitudinal section; B, the same entire. (A, B enlarged after Solms-Laubach.) C, D, a yam (*Dioscorea bonariensis*), enlarged (after Beccari). E-G, embryos of "monocotyledonous dicotyledons;" E, the water chestnut (*Trapa natans*), half size (after Barneoud); F and G, Butterworts (*Pinguicula vulgaris* and *P. caudata*), after Dickson, both greatly enlarged.

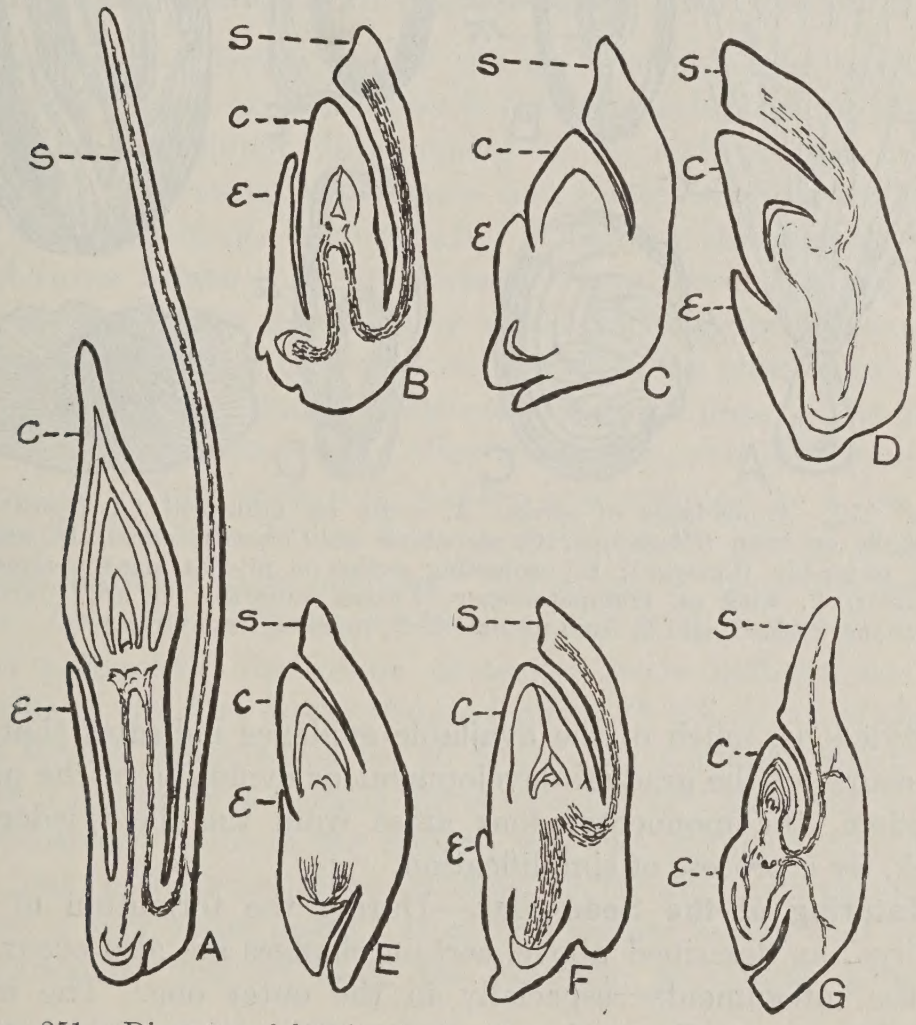


FIG. 251.—Diagram of longitudinal sections of grass-embryos (Gramineæ) to illustrate the rudimentary cotyledon (*epiblast*). A–C, E–G, redrawn from J. M. Coulter, after Bruns; D, from nature. A, *Zizania aquatica;* B, *Leersia clandestina;* C, *Leptochloa arabica;* D, *Triticum vulgare;* E, *Spartina cynosuroides;* F, *Triticum vulgare;* G, *Zea Mays; s*, scutellum; *c*, coleoptile; *e*, epiblast.

his two great classes of "flowering herbs." He was also one of the few early botanists to recognize the existence of sex in plants.

Either type of embryo may develop more or less imperfectly, so that we have *monocotyledonous dicotyledons* or *dicotyledonous monocotyledons* (Fig. 250). In many of the monocotyledonous grass-embryos (*e.g.* Indian corn, wheat, and others) traces of a second cotyledon occur as a rule (Fig. 251). While the monocotyledons are more simply organized, anatomically, than the

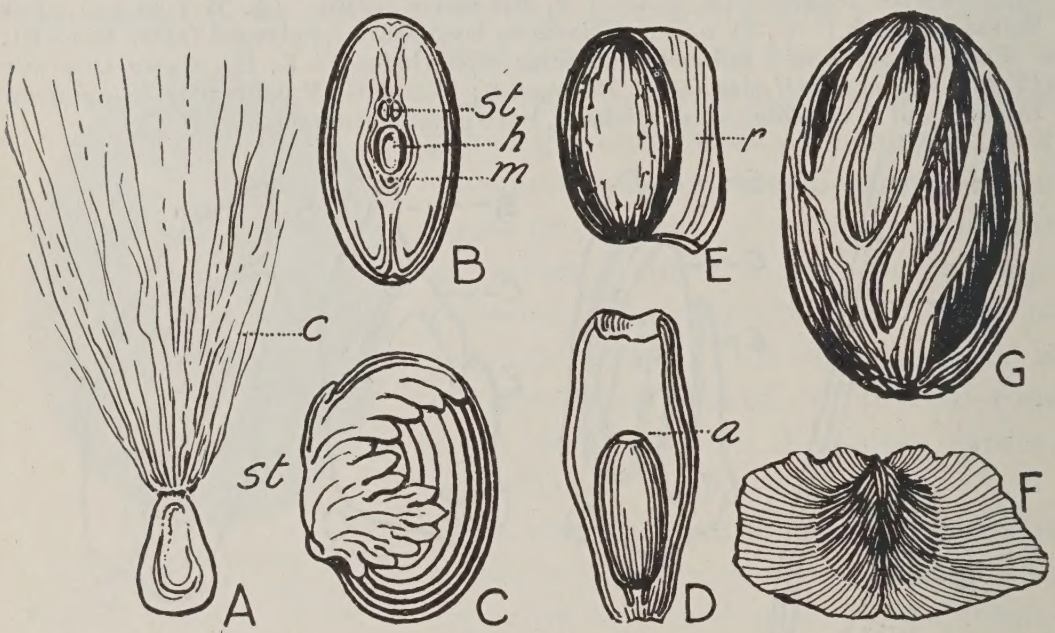


FIG. 252.—Appendages of seeds. A, coma on milkweed (*Asclepias*); B, strophiole on bean (*Phaseolus*); C, strophiole on *Corydalis aurea;* D, aril on white water-lily (*Castalia*); E, projecting raphe on pitcher plant (*Sarracenia purpurea*); F, wing on trumpetcreeper (*Tecoma radicans*); G, aril ("mace") on nutmeg. (A, B, and G from nature; C–F, redrawn from Gray.)

dicotyledons, much of the available evidence indicates that, in the course of the gradual development or evolution of the plant kingdom, the monocotyledons arose from the dicotyledonous stock, by a process of simplification.

Maturing of the Seed-coat.—During the formation of the embryo, as described above, certain changes are also occurring in the integuments—especially in the outer one. The inner integument usually undergoes very little change, and often adheres so closely to the outer integument that the two cannot be easily distinguished in the mature seed.

The outer integument commonly becomes hard, and is hence called the *testa*. It frequently develops certain outgrowths: a *wing* in the Trumpetcreeper (*Tecoma*); a tuft of hair (the *coma*) in milkweed; long hairs of commercial use in the cotton seed; an appendage, *strophiole*, at the base, near the hilum; a somewhat similar appendage, the *caruncle*, about the micropyle; an outgrowth from the stalk of the ovule, called the *aril*, as in the white waterlily. In the red currant (*Ribes vulgare*) the seed is covered by a generalized aril. The aril of the nutmeg seed forms the "*mace*" of commerce. These structures are all illustrated in figures 252,[1] and 440 (caruncle).

SECONDARY RESULTS OF POLLINATION AND FERTILIZATION

Immediate Effect of Pollen.—As we have just seen, one of the ultimate effects of pollination is the fertilization of an egg-cell, and the consequent development of an embryo and a seed. Equally interesting is the more immediate effect of the pollen on the flower itself. Shortly after pollination the stigma withers and turns brown. In some cases, where the pollen begins to germinate almost immediately after reaching the stigma, this change will occur within an hour, but when the pollen germinates more slowly the change may not occur for days. The petals lose water and wither soon after the stigma, and then gradually drop off. Their withering is often accompanied by a loss or a change of color. It has been experimentally proved that the pollen initiates these changes. For example, of two flowers of flax (*Linum grandiflorum*) which opened at the same time, one was pollinated, the other protected from pollination. The corolla of the first flower dropped off in 35 hours, while that of the second remained on for 80 hours. In a similar experiment with a species of *Anagallis* the corolla fell in 4 days and 6 days, respectively. One of the reasons why cut orchids remain fresh so long is because under artificial cultivation pollination seldom, if ever, takes place. It is for a similar reason that double (cultivated) flowers, such, for example, as double geranium

[1] The wings of maple, ash, and elm "seeds," and the *pappus* of hairs on the "seeds" of such plants as thistle and dandelion are outgrowths of the ovary, the so-called "seeds" being, in reality, not seeds but ripened ovaries, each containing one seed.

(*Pelargonium*), tulips, carnations, stocks, roses, and others remain fresh so long.

Carpotropic Movements.—In many plants the first noticeable effect of pollination is a change in the attitude of the flower. This is strikingly illustrated in the Alsike Clover (*Trifolium hybridum*). The flower buds in the head are nearly or quite upright, and remain so after *anthesis*, or the first opening of the flower buds. The petals are also predominantly white. Soon after pollen has been deposited on the stigma, however, the upper side of the pedicel begins to grow in length, resulting in the bending down of the floret. This occurs in each of the florets as, one after the other, they are visited by the bees, until finally all, or nearly all, of them are bent over. During this change the petals gradually become a deep pink color, but finally, as the flowers wither, the petals turn brown (Cf. Figs. 185, and 186. See also p. 7).

Formation of Fruit.—In the majority of plants the ovary, in the absence of pollination, never undergoes change beyond its condition in the full-blown flower; but in all plants, after pollination, the ovary, and often adjacent parts such as the calyx, receptacle, and peduncle, undergo morphological changes and thus become transformed into what is known as the "fruit." This is strikingly shown in the apple. The floral organs develop on the *torus*, or at the end of the floral axis, in *acropetal succession*, that is, the outer circle of sepals first, the central carpels last. As the flower develops (Fig. 253), the receptacle or torus becomes concave, growing up around the ovary, with the calyx tube in advance bearing the stamens and petals. With the maturing of the flower all growth of these parts ceases, until and unless pollination and fertilization occur. In that event the receptacle continues or resumes its growth, forming the fleshy, edible portion of the fruit, with the calyx and stamens at the "blow" end, and the tips of the styles protruding.

That these changes are the result of pollination may often be seen in imperfect fruit, not only of apples, but also of the tomato, pumpkin, and other species where fertilization has occurred in only one or more (but not all) of the carpels. In such cases, only the carpels whose ovules were fertilized mature normally (Fig. 254).

Just how the stimulus to fruit development is brought about or transmitted to the parts involved is not definitely known.

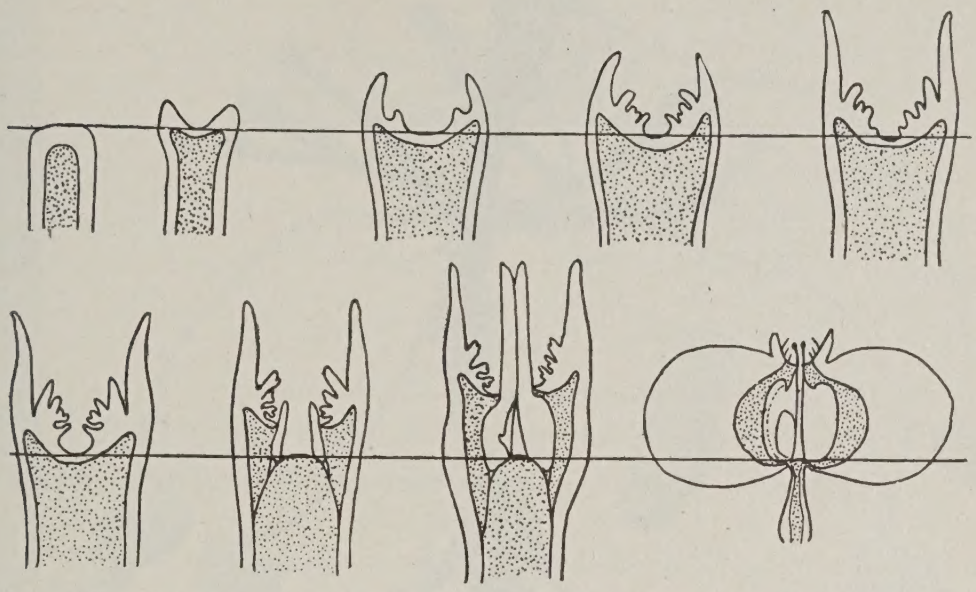


FIG. 253.—Diagram showing the development of the apple. The dotted area represents pith. Not drawn to scale. (After Kraus, Oregon Agr. Exp. Sta.)

It may be that, as the result of fertilization, some growth-promoting enzyme or some hormone is formed and diffuses out into the surrounding tissues.

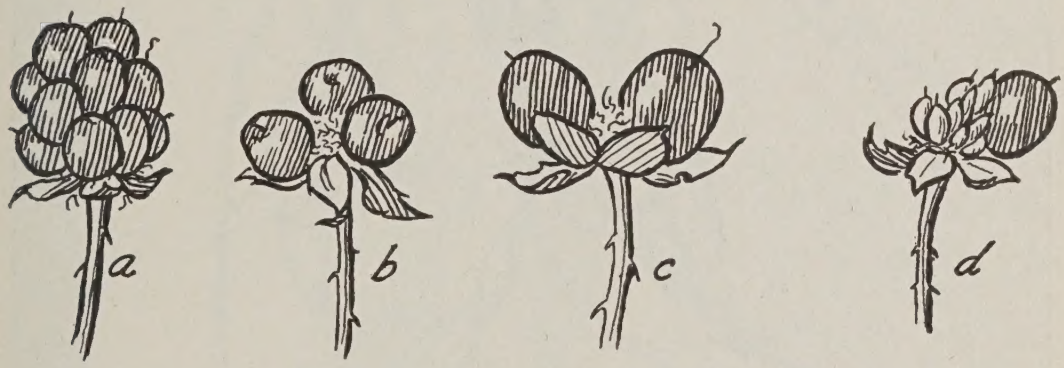


FIG. 254.—Fruits of a wild blackberry (*Rubus*). This is an *aggregate* fruit, consisting of a number of ripened ovaries (drupes) of the same flower crowded on a fleshy receptacle. In *a* all the pistils were pollinated and so all the ovaries ripened into drupes, forming a perfect, symmetrical fruit. In *b* only three, in *c*, only two, and in *d* only one of the pistils were pollinated. The undeveloped ovaries are clearly shown in *d*. The one that had been pollinated was large, sweet, and juicy. Note the remains of the styles on the ovaries, and also the persistent calyx. (Drawn from nature by Elisabeth Telling.)

The *peanut* (*Arachis hypogea*) affords an interesting illustration of the secondary effect of fertilization. The flowers grow near

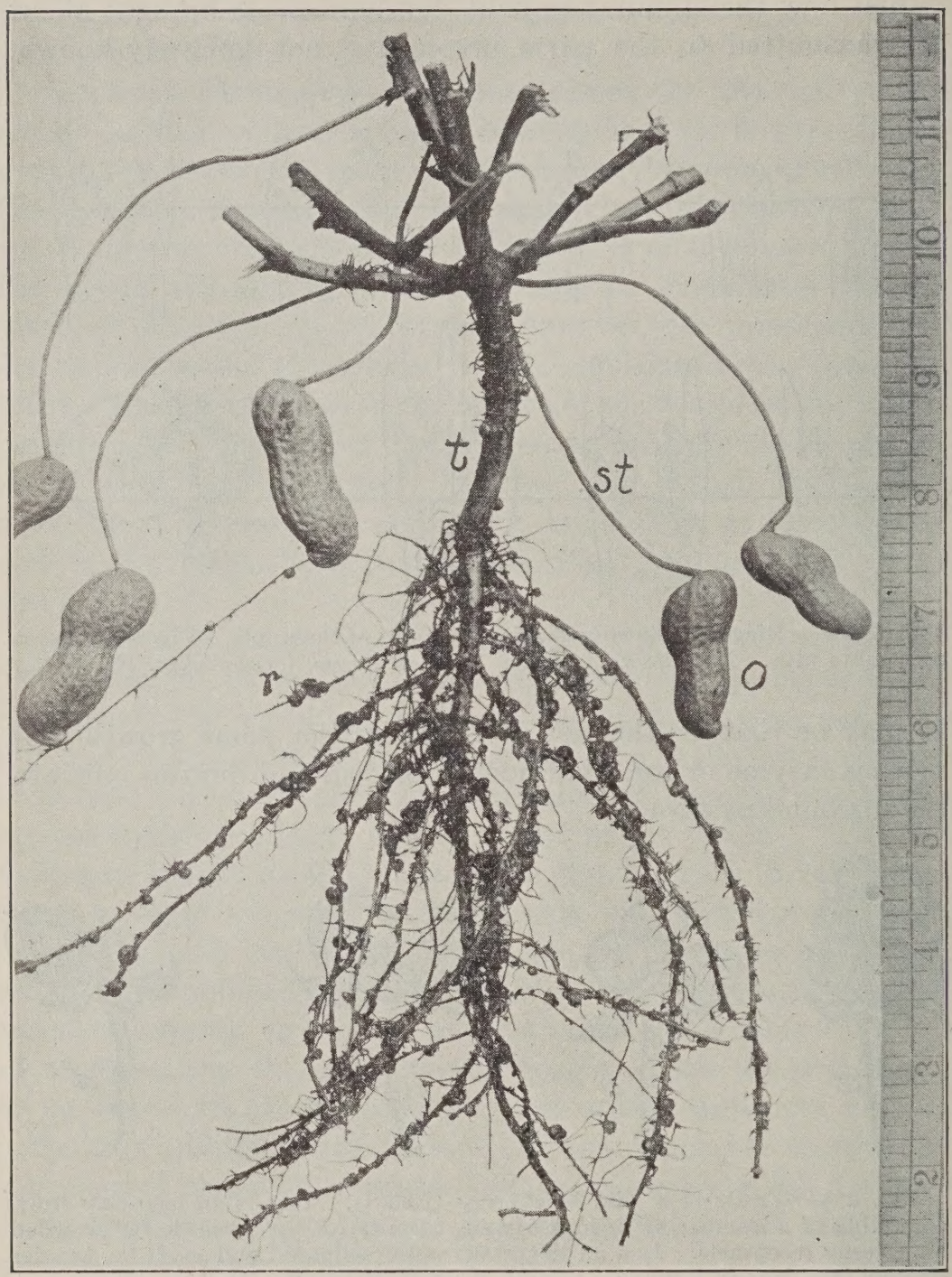


FIG. 255.—Portion of a Peanut plant (*Arachis hypogaea*), showing roots, and the lower portion of the shoot from which have grown the ripening ovaries (peanuts) in various stages of development. *t*, tap-root, bearing lateral roots and rootlets on which are numerous leguminous tubercles, as at *r*; *st*, elongated ovary-stalk or stipe; *o*, ripened ovary or peanut. (After Beattie, U. S. Dept. Agr. Farmers Bull. No. 431.)

the ground, and after fertilization has taken place the corolla and stamens fall away and the stipe or stalk of the ovary

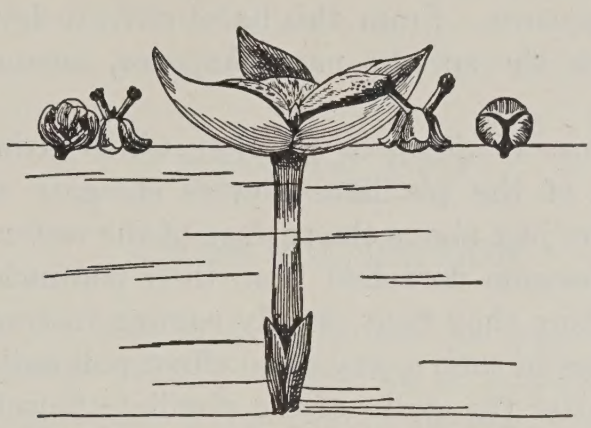


FIG. 256.—Flowers of the Eel Grass. A staminate flower (on the right) has floated against the larger pistillate flower and one of the anthers is in contact with a stigma, thus effecting pollination. (From Stevens, after Kerner.)

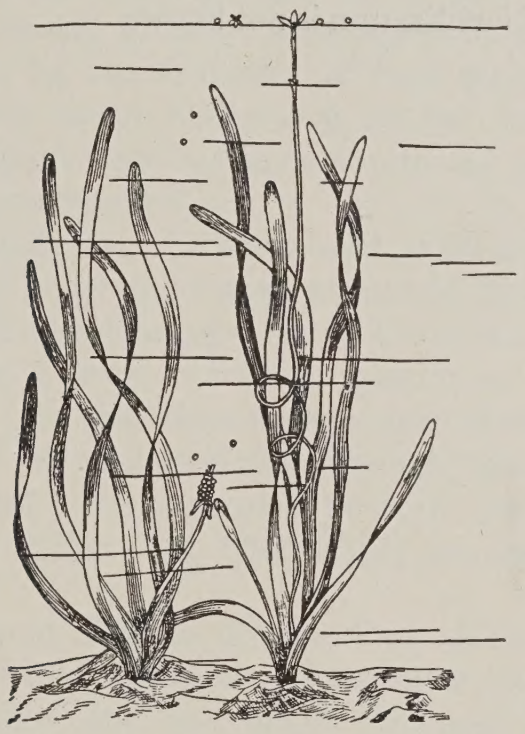


FIG. 257.—Eel Grass (*Vallisneria spiralis*). The plant on the left has staminate flowers which become free and rise to the surface of the water. The right hand plant bears a pistillate flower which floats on the surface but remains attached to the flower-stalk. After pollination this flower is drawn down near the bottom by the coiling of the flowerstalk. (From Stevens, after Kerner.)

(Cf. p. 631) begins to elongate, growing more rapidly on the upper side, and thus eventually carrying the ovary below the

surface of the soil. In this environment the ovary ripens into the fruit or "peanut (Fig. 255)," but otherwise it merely shrivels and fails to mature. From this habit of fruit development the peanut receives the specific name *hypogea*, meaning "beneath the ground."

In the *Eelgrass* (*Vallisneria spiralis*), which grows submerged, the peduncles of the pistillate flowers elongate sufficiently to raise the flowers just above the surface of the water. The staminate flowers become detached from their peduncles and rise to the surface where they float, finally coming in contact with the pistillate flowers in such a way as to effect pollination (Fig. 256). Shortly thereafter the stalks of the pistillate flowers form a coil, thus drawing the flowers under the surface of the water where the seeds develop (Fig. 257). Whether the stimulus that causes the coiling of the flower stalk results from pollination alone, or is a consequence of fertilization is not known.

CHAPTER XVII

CROSS-POLLINATION

Historical.—It is an interesting fact that men studied and cultivated plants for literally thousands of years before they discovered the functions of the various organs of the flower, and especially that of pollen. For centuries the Arabs and others knew that a certain practice, known as caprification, was necessary in order to secure Smyrna figs. It is now known that that practice is necessary in order to secure pollination, upon which, in the Smyrna fig, the formation of fruit depends; but the true explanation was never understood by the Arabs, and in fact could not be understood by anyone until the parts of the flower were correctly interpreted.

Now the significance of stamens and pistils and floral envelopes was not really understood until as late as the year 1694, when Rudolph Jacob Camerarius wrote to his friend, Professor Valentin, in Giessen, a letter, "*De sexu plantarum*" (Concerning the sex of plants). In this letter the structure of the flower is clearly described, and the various parts, especially the anthers and pollen, interpreted. His experiments with the castor-oil plant (*Ricinus*) and Indian Corn (*Zea Mays*) are described in the following words:

"In the second division of plants, in which the male flowers are separated from the female on the same plant, I have learnt by two examples the bad effect produced by removing the anthers. When I removed the male flowers (*globulos*) of *Ricinus* before the anthers had expanded, and prevented the growth of the younger ones, but preserved the ovaries that were already formed, I never obtained perfect seeds, but observed empty vessels, which fell finally to the ground, exhausted, and dried up. In like manner I carefully cut off the stigmas of *Mais* that were already dependent, in consequence of which two ears remained

entirely without seeds, though the number of abortive husks (*vesicularum*) was very great."[1]

But while Camerarius recognized that the presence of anthers is necessary for the formation of seeds, his conception of the part they play was wholly erroneous, for he considered that the anthers "prepared beforehand the young plant contained in the seed."

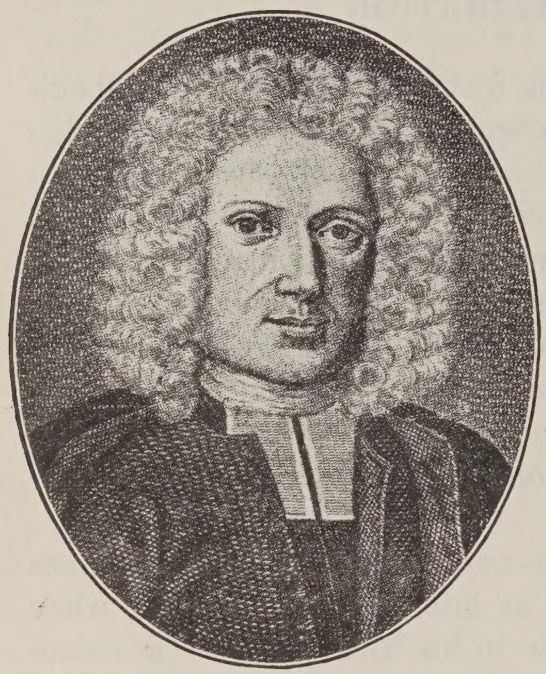


FIG. 258.

FIG. 259.

FIG. 258.—Rudolph Jacob Camerarius (1665–1721). By three years of careful experimenting he was one of the first to demonstrate the sexuality of plants, and the necessity of pollination for the formation of seeds.

FIG. 259.—Joseph Gottlieb Koelreuter (1733–1806). Early investigator of the problem of the sexuality of plants, and one of the first to explain the purpose of nectar and the function of insects in pollination. He produced the first plant hybrids.

Over 60 years after Camerarius wrote his letter, Joseph Gottlieb Koelreuter (1761) began to publish his "*Preliminary account of a few investigations and observations concerning sex in plants.*" The pollen-tube had not then been discovered, and Koelreuter thought that the pollen grains supplied an oily fluid which was supposed to unite with a similar substance secreted by the stigma and, in some manner, not well understood,

[1] Quoted from Sachs's *History of Botany*, Eng. Translation by Garnsey and Balfour (p. 387).

found its way down the style and finally to the ovule. In Koelreuter's mind this union of the two oily fluids on the stigma constituted the real act of fertilization. Far as he was from the truth, he came nearer to it than any previous student of plants had ever come, and his hypothesis made it possible to understand with some degree of intelligence the matter of cross-pollination.

In Chapter XV we have traced the processes by which seeds are made and have seen that, while in some plants the essential floral organs occur on the same flower, or on different flowers of the same plant (*monoecious* plants), in other plants staminate flowers and pistillate flowers are found on different individuals—that is, the plants are *dioecious*. Obviously, in the latter case, pollination can be secured only by the transfer of pollen from one plant to the other. Here again the keen observation of Koelreuter came into play, and he was one of the first botanists to recognize and describe the part played by insects in pollination. "In flowers in which pollination is not produced by direct contact in the usual way," says Koelreuter, "insects are as a rule the agents employed to effect it, and thus to bring about fertilization." By this statement of Koelreuter's we are introduced to one of the most fascinating chapters of botany—the relation between insects and flowers.

The next outstanding name is that of Christian Konrad Sprengel, whose remarkable book, "*Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen,* appeared in 1793.[1] In this book Sprengel recognizes the importance of cross-pollination and, for the first time, perceives that the flower can really be understood only in connection with the visits of insects by which cross-pollination is accomplished. This book was the forerunner of many others, culminating with the scholarly works of Darwin, Kerner, Müller, Knuth, and others.[2]

[1] Charles Darwin's Autobiography contains the following statement: ". . . my interest in insect pollination was greatly enhanced by having procured and read in 1841, through the advice of Robert Brown, a copy of C. K. Sprengel's wonderful book, '*Das entdeckte Geheimniss der Natur*'."

[2] Darwin, Charles. *On the various contrivances by which orchids are fertilized by insects.* London, 1862.

Darwin, Charles. The different forms of flowers on plants of the same species. London, 1877.

Types of Cross-pollination.—*Self-pollination*, that is, the pollination of a stigma by pollen from the same flower, is of course possible only with perfect (hermaphrodite) flowers. In the case of *cross-pollination*, the stigma receives pollen from another flower. Three types are recognized, though they differ in degree rather than in kind, as follows:

1. The stigma receives pollen from another flower of the same plant. Kerner called this *Geitonogamy*, from the Greek meaning "pollination by a neighbor;" that is, by a near-by or neighboring flower.

2. The stigma receives pollen from a flower of another plant of the same species. This was called by Kerner *Xenogamy*, meaning "pollination by a guest." This is also called *crossing*.

3. The stigma receives pollen from a flower of a different species of plant. This is a special case of crossing, and the term *hybridizing* is sometimes confined to crossing between species, the offspring of the cross being hybrids. In the modern literature of genetics, however, the term hybrid is not confined to the offspring of crosses between species, but is applied also to the offspring of crosses between varieties—in fact to the offspring of any cross.

Economic Bearings of Cross-pollination.—Before discussing the various means by which cross-pollination is secured, a few instances may be mentioned showing the economic importance of this process and of a knowledge of it. The date-palm is particularly interesting in this connection. Pliny noted that this palm is dioecious, that is, it has both fruit-bearing (pistillate) and non-fruit bearing (staminate) trees. Normal pollination is by wind, but in a plantation of cultivated dates the laborers must climb the staminate trees to secure staminate blossoms, then climb the pistillate trees and dust the naked ovules with the pollen. It is said that, during Napoleon's campaigns in Egypt, the date crop about Cairo was nearly a failure because the men

---

Kerner, A. *Flowers and their unbidden guests.* Eng. trans. With a prefatory letter by Charles Darwin. London, 1878.

Müller, Hermann. *The fertilization of flowers.* Eng. trans. With a preface by Charles Darwin. London, 1883.

Knuth, Paul. *Handbook of flower pollination.* Eng. trans. by J. R. Ainsworth Davis. 3 vols. Oxford, 1906–1909.

who attended to the work of pollination were nearly all in the army and the pollination was, consequently, largely neglected.

"In the East, dates are such an important article of food, and the failure of the crop such a serious loss, that nations at war, and desirous of inflicting as much injury as possible upon one another, were in the habit of cutting down, not all the palms indiscriminately, but those bearing pollen."[1] It is said that during a certain war, the Persians collected a large quantity of pollen from their staminate trees and kept it concealed until the war was over. This, of course, would have been of no avail except for the long

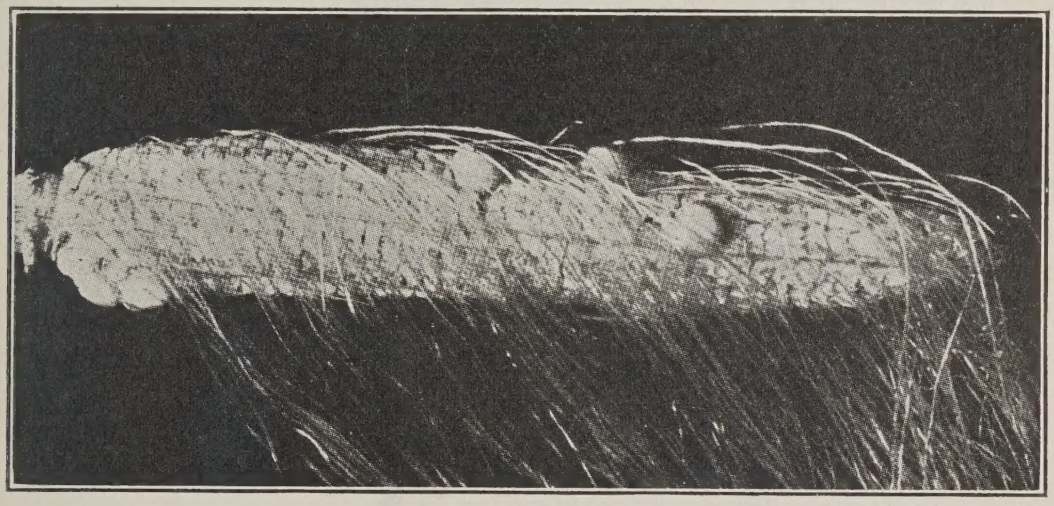


FIG. 260.—An ear of corn borne by an isolated stalk, showing lack of cross-pollination. (Yearbook U. S. Dept. Agr., 1905.)

period of viability of date pollen (2–18 years, *fide* André Michaux, quoted by Fourcroy, A. F. *Ann. Mus. Nat. Hist. Nat.* **1**: 417. 1802). (Cf. also, p. 870.)

The disastrous effects on the yield of a corn crop when cross-pollination is prevented are illustrated by figure 260, which represents an ear borne by an isolated plant, so that cross-pollination was not possible. Only five or six kernels on the entire ear developed toward maturity, since most of the "silks," that bear the stigmatic surfaces, were not in a condition to receive the pollen from the same plant at the time the anthers (on the tassel) discharged it.[2]

[1] Gaye, Selina. The great world's farm. London, 1894.

[2] Shamel, A. D. The effect of inbreeding in plants. Year Book U. S. Department Agr. **1905**: 377–392. 1906. The term "inbreeding" is used

Effect of Cross-pollination on Yield.—The effect of cross-pollination on yield falls under two heads:

Fig. 261.—Effect of self-pollination in the blueberry (*Vaccinium corymbosum*), as compared with cross-pollination. These two twigs, both natural size, were in equally good situations on the same bush, contained the same number of flowers, all pollinated by hand at the same time with equal care, and the fruits were photographed on the same day. The only difference in treatment was that the pollen used on the left-hand twig came from other flowers on the same bush, while the pollen for the right-hand twig was taken from another bush. The self-pollinated flowers produced no ripe fruit, all the fruit that set remaining small and green and later dropping off, until at the time the photograph was taken only two such imperfect fruits remained. A plantation made up wholly from cuttings from a single bush would produce little or no fruit. At least two original propagation stocks are necessary. (After Coville. Courtesy of the U. S. Dept. Agric.)

a. The effect on the size of the fruit produced by the cross-pollinated flowers themselves. One of the most striking illustrations

---

by Shamel to mean, "the fertilization of a flower with its own pollen, with pollen from another flower on the same plant, or with pollen from a closely related plant." Some writers limit the term to the first two of these three alternatives.

of this is found in the experiments of Coville[1] on the blueberry (*Vaccinium*), as illustrated in figure 261. The two twigs shown in the figure "grew in equally good situations on the same bush, contained the same number of flowers, all pollinated by hand with equal care, and the flowers were pollinated on the same day. The only difference in treatment was that the pollen used on the left-hand twig came from other flowers on the same bush, while the pollen for the right hand twig was taken from another bush . . . A plantation made up wholly from cuttings from a single bush would produce little or no fruit. At least two original propagation stocks are necessary . . . a row of plants from one stock being followed by a row from the other."[2]

b. Effect on the Yield of the Crop Grown from Seeds Produced by Cross-pollinated Flowers.—In 1876 there appeared Charles Darwin's book, "*The Effects of Cross and Self Fertilization in the Vegetable Kingdom.*"[3] This classic treatise, of 469 pages, embodies the results of studies that extended over eleven years, though the general subject of cross-pollination had been a matter of interest to Darwin for thirty-seven years. He was led to his experimental studies on the effects of cross-pollination on progeny by an accidental observation "that seedlings of self-fertilized parentage are inferior, even in the first generation, in height and vigour to seedlings of cross-fertilized parentage." Experimenting with plants, cultivated and wild, and representing a wide range of plant families, he found that, as a general rule, plants resulting from a cross excelled those resulting from self-fertilization (*selfing*) in height, weight, rate of germination, early flowering, general constitutional vigour, yield of seed, and other characters. More recent experiments have tended, in general, to confirm Darwin's results.

The high-bush blueberry (*Vaccinium corymbosum*) may be cited again in this connection. Coville[4] finds that, by selecting

[1] Coville, F. V. Directions for blueberry culture, 1921. U. S. Dept. Agr. Bull. 974. Washington, 1921.

[2] Coville, *l. c.*

[3] The word "fertilization" was used by Darwin, and other earlier writers in the sense of "pollination." The term "fertilization," as now used, refers to the fusion of the egg- and sperm-cells.

[4] *Loc. cit.*

the best individuals *produced by crossing* plants chosen for large size and other desirable qualities of fruit, and propagating these by cuttings, the size of the fruit may be increased from that of a garden pea to nearly one inch in diameter. On the other hand, when flowers of large-fruited varieties are pollinated from small-fruited wild plants the resulting seedlings combine the inferior characters of the wild plants with those of the variety.

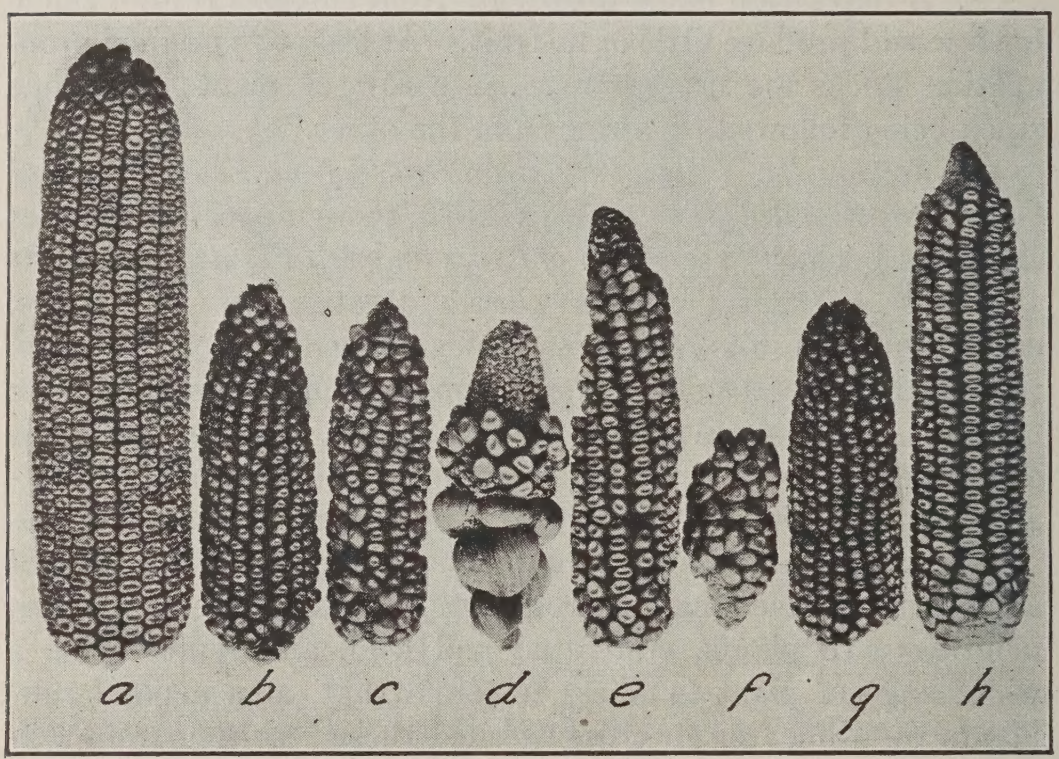


FIG. 262.—At left (*a*) typical ear of Hogue's Yellow dent corn; *b-h*, typical ears of seven distinct pure lines of the same variety after six years of self-pollination. The yields of these strains per acre were; *a*, 37.5 bu., *b*, 10.8 bu., *c*, 8.0 bu., *d*, 3.1 bu., *e*. 14.5 bu., *f*, 2.3 bu., *g*, 15.4 bu., *h*, 14.8 bu. (Cf. Fig. 263). (After Kiesselbach, Univ. Nebraska Agr. Exp. Sta. Res. Bull. No. 20, 1922.)

Experiments of several investigators have shown that the yield of Indian corn is greatly diminished by close pollination (inbreeding), but is greatly increased in the first generation cross between inbred strains. Thus, for example, Kiesselbach,[1] in 1908, by close-pollinating, produced twelve inbred strains of Hogue's Yellow Dent corn. In 1911, after four years, four of these strains

[1] Kiesselbach, T. A. Corn investigations. Univ. Nebraska Agr. Exp. Sta. Research Bull. No. 20. 1922.

had become sterile and so came to an end. A fifth became sterile four years later (1915). Typical ears borne by the seven remaining strains are shown in Fig. 262. The yield of the original

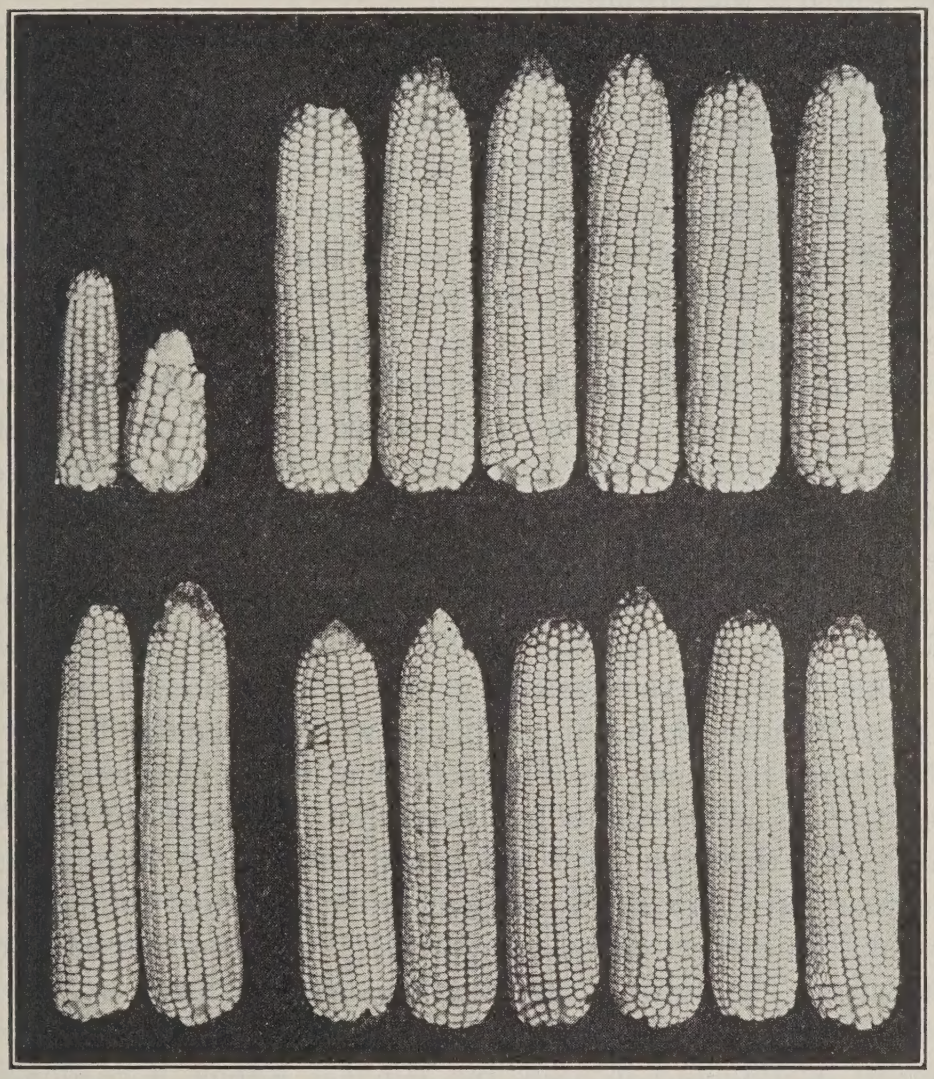


FIG. 263.—Representative ears of corn (*Zea Mays*), Hogue's Yellow Dent variety, showing the effects of prolonged inbreeding, followed by crossing the homologous pure lines. Lower row, the original commercial seed at the left; the progeny of their cross at the right. Upper row, at the left parents resulting from six years of inbreeding; at the right the first generation, hybrid progeny. (After Kiesselbach, Univ. Nebraska Agr. Exp. Sta. Res. Bull. No. 20.) (Cf. Fig. 262.)

Hogue's Yellow Dent was 37.5 bushels per acre; the average yield of the seven inbred strains was 9.8 bushels.

The inbred strains were then cross-pollinated in various combinations and the yield of the first generation hybrids averaged 51.7 bushels per acre, an increase of 138 per cent. (Fig. 263).

This increase, however, does not persist beyond the first hybrid generation, for the yield of the second generation hybrid (inbred) was only 25.1 bushels, or only 67 % as much as the original variety from which it was produced.

The "Strawberry War."—In the early days of strawberry culture success was more or less uncertain because growers were ignorant of the fact of sex in plants, and did not know that the strawberry was dioecious or polygamo-dioecious. Nor was this knowledge readily accepted and acted on when pointed out, and the period from 1842–1848 witnessed what was known as the "strawberry war"—a war of words—over the question as to the real secret of success in securing large yields. The wild species have, in general, perfect flowers, but under cultivation the polygamo-dioecious habit developed, some plants bearing flowers with aborted stamens, and therefore being incapable of self-pollination. Other plants of cultivated varieties, notably the Hautbois, bore only staminate flowers. This observation was first noted by the well-known French botanist, Duchesne,[1] in 1766. The Hautbois was popularly supposed to be running out, but Duchesne, on the basis of careful observation, showed that this was because the staminate plants were systematically weeded out of the beds since they were known not to bear fruit. This left little or no pollen to pollinate the flowers of the pistillate plants, and thus the yield was greatly reduced. This observation was quite contrary to the generally accepted notions of his day, and Duchesne received a reprimand from his former teacher Linnaeus. The information was at once utilized by French growers, but was disregarded in other countries. It was rediscovered in England in 1809 by Michael Keens, a gardener of Isleworth. When cultivated varieties were introduced into America from England this knowledge was generally unknown or disregarded, although it was published in the "American Gar-

[1] Antoine Nicolas Duchesne. *b.* Versailles, Oct. 7, 1747; *d.* Paris, Feb. 18, 1827. A pupil of Linnaeus. The genus Duchesnea, of the Rose Family, was named after him. His monograph on the strawberry was entitled *Histoire Naturelle des Fraisiers, contenant les vues d'economie reunies à la botanique*, etc. (Natural history of the strawberry, from both an economic and a botanical point of view.) Paris, 1766. The French name for the plant (*Fraisier*) is from the French officer (*Frezier*) who introduced the Chilean species into Europe.

dener's Calendar" (1806), and by William Prince, proprietor of the famous nurseries at Flushing, L. I., in his "Short Treatise on Horticulture."

The strawberry crop came to be regarded as a fickle one, until 1842 when Nicholas Longworth fired the first gun in the so-called "strawberry war." Longworth published a letter in the Magazine of Horticulture calling attention to the imperfect nature of the flowers, and the consequent necessity of growing both staminate and pistillate plants in the same bed. All the other leading growers in the country disputed this, including Hovey, who originated the Hovey variety. The contest involved three questions:[1]

1. Are there pistillate varieties that must be planted near pollen bearing sorts in order to be fruitful?

2. Can the "sex" of a variety be changed from staminate to pistillate by culture (abundant fertilizer, etc.)?

3. Are pistillate varieties, planted by themselves, more productive and valuable than staminate sorts?

The "war" continued as a war of words so long as the contestants continued merely to express "opinions" not based on careful observation and experiment. Finally the question was settled by the report of J. A. Warder, secretary of the Cincinnati Horticultural Society, and it should be emphasized that the finality of his report depended upon the fact that, in preparation for writing it, Warder examined "millions of blossoms."[2] Hovey and all other opponents were convinced. The first of the above three questions was answered affirmatively, the last two negatively. The strawberry growers owe a great debt of gratitude to Longworth and Warder for the solution of this puzzling question which insured the success of strawberry culture in America.

How Cross-pollination Is Insured.—Among the various methods by which cross-pollination is insured are the following:

a. Dioecious Habit.—Staminate flowers and pistillate flowers borne on different plants. This is the case, in part, with the strawberry (as noted above), date, yew, hemp, poplar, willow, certain cucurbits (sometimes), and other plants.

[1] Summary from Fletcher, S. W. *The strawberry in North America.* New York, 1917. This work has been freely drawn on in the above account.

[2] *The Country Gentleman,* 1854, p. 267.

b. Monoecious Habit.—Staminate and pistillate flowers borne on the same plant. This, of course, prevents the selfing of any individual flower, but not the self-pollination of the plant as a whole, unless some one or more of the factors mentioned below enter in. Among monoecious plants may be mentioned the pine, walnut, hickory, various cucurbits (*e.g.*, pumpkin, *Cucurbita pepo*, and watermelon, *Citrullus vulgaris*), cat-tail, Jack-in-the-pulpit, calla lily, begonia, castor-oil plant, Indian corn, and many more.

c. Stigma Sterile.—In certain species the pollen cannot germinate on stigmas of flowers of the same plant that produces the pollen. This condition obtains in the rye. Barley and wheat, however, are largely self-fertilized.

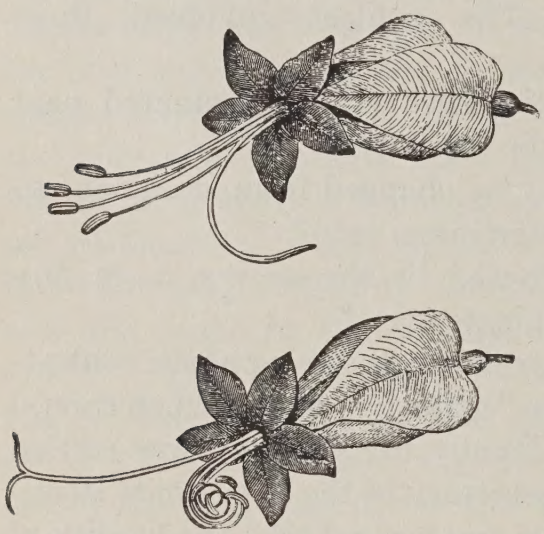


FIG. 264.—Flowers of the Glory Flower (*Clerodendron*), showing *proterandry*. Above, the stamens are mature, but not the stigma; below, the stigma has become receptive after the stamens have shed their pollen. (Redrawn from Gray.)

d. Stigma Poisonous.—In certain orchids the secretion of the stigma of each flower is toxic to the pollen of flowers on the same plant.

e. Pollen Poisonous.—In certain orchids, again, the pollen of a given flower is apparently toxic to the flower, causing it to wither and fall off.

f. Stamens Mature First.—This would insure pollination from another flower, but not necessarily from another plant. This is common in geranium, composites (sunflower, lettuce, thistle), Indian corn, as a rule, and other plants. It is termed *proterandry*. Asa Gray has described the exceedingly interesting proterandry of the "Glory Flower" (*Clerodendron*) in the following words:

"The adaptations in this flower . . . are exquisite. The crimson corolla and bright white calyx in combination are very conspicuous. The long filiform filaments and style, upwardly enrolled in the bud, straighten and project when the corolla opens: the stamens remain straight, but the style proceeds to curve downward and backward, as in figure 264 (upper figure). The

anthers are now discharging pollen: the stigmas are immature and closed. Fig. 264 (lower figure) represents the flower on the second day, the anthers effete, and the filaments recurved and rolled up spirally; while the style has taken the position of the filaments, and the two stigmas now separated and receptive are in the very position of the anthers the previous day. The entrance by which the proboscis of a butterfly may reach the nectar at bottom is at the upper side of the orifice. The flower cannot self-fertilize. A good-sized insect flying from blossom to blossom, and plant to plant, must transport pollen from one to the stigma of the other."[1]

g. Stigma Matures First.—This is termed *proterogyny*, and is, apparently, not so common as proterandry. It is illustrated in

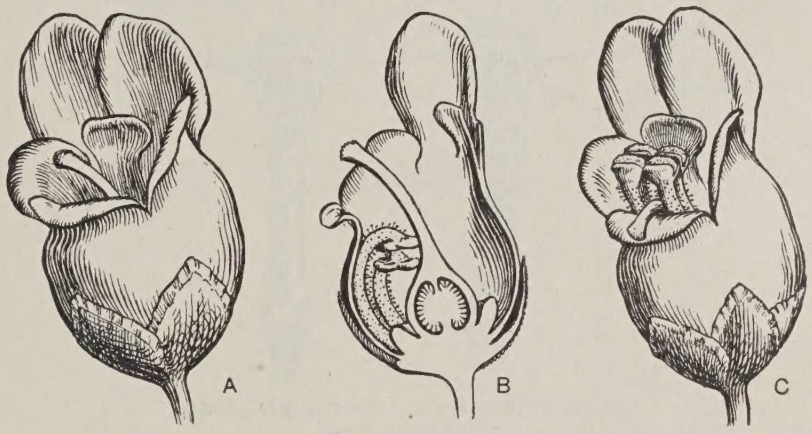


FIG. 265.—Flowers of the Figwort (*Scrophularia nodosa*). The two at the left recently opened, showing *proterogyny*. At the right a flower a few days older, showing the stamens mature after the stigma has passed maturity. (Modified from Baillon.)

the common Plantain (*Plantago*), Magnolia, Scrophularia (Fig. 265), and others. In *Avocado* orchards this behavior occurs *en masse* or synchronously throughout the orchard.

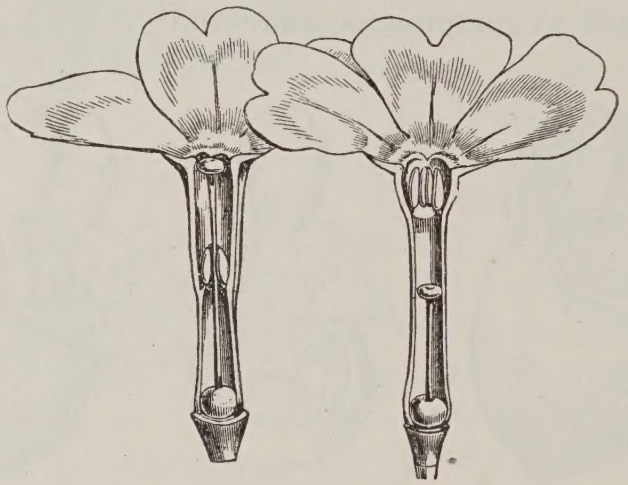
In the Skunkcabbage (*Symplocarpus*) some plants are proterandrous, some proterogynous, and in yet others both conditions may be found at the same time in different flowers.

h. Heterostyly.—"No little discovery of mine," said Charles Darwin, "ever gave me so much pleasure as the making out of the meaning of heterostyled flowers." The fact of heterostyly had been known to botanists long before Darwin, but it was he who

[1] Gray, Asa. Structural Botany. p. 220–221. New York, 1879.

first studied it systematically and discovered its true significance. It is well illustrated in the Partridgeberry (*Mitchella repens*). A classic example is the Primrose (*Primula veris*, var. *officinalis*), whose heterostyly was first noted by the early American botanist, Persoon. The two types of flower are illustrated in Fig. 266, and their structural differences are thus summed up by Darwin:

"The long-styled plants have a much longer pistil, with a globular and much rougher stigma, standing high above the anthers. The stamens are short; the grains of pollen smaller and oblong in shape. The upper half of the tube of the corolla is more expanded. The number of seeds produced is smaller and



Long-styled form, Short-styled form
PRIMULA VERIS.

FIG. 266.—Flowers of a Primrose showing heterostyly. (After Darwin.)

the ovules larger. The plants tend to flower first" (*i.e.*, before the short-styled plants).

"The short-styled plants have a short pistil, half the length of the tube of the corolla, with a smooth depressed stigma standing beneath the anthers. The stamens are long; the grains of pollen are spherical and larger. The tube of the corolla is of uniform diameter except close to the upper end. The number of seeds produced is larger" (than those of the long-styled plants). The larger pollen-grains of the short-styled plants were to those of the long-styled plants in the ratio of 100 to 67 in number.

Darwin tried the effect of the four different unions possible in pollination,[1] and found that, in every case, when the two forms of

[1] The student should indicate what these four possibilities are. Darwin called two of them *legitimate*, and two *illegitimate*.

flower were crossed ("legitimate" union) more flowers produced fruit and better fruit, and the seeds weighed more than when the flowers were selfed ("illegitimate" union) (Fig. 267).

From these and many other similar experiments Darwin inferred the meaning of heterostyly, as follows: "The benefit which heterostyled dimorphic plants derive from the existence of the two forms is sufficiently obvious, namely, the intercrossing of distinct plants being thus assured." "No doubt," he says, "pollen will occasionally be placed by insects or fall on the stigma

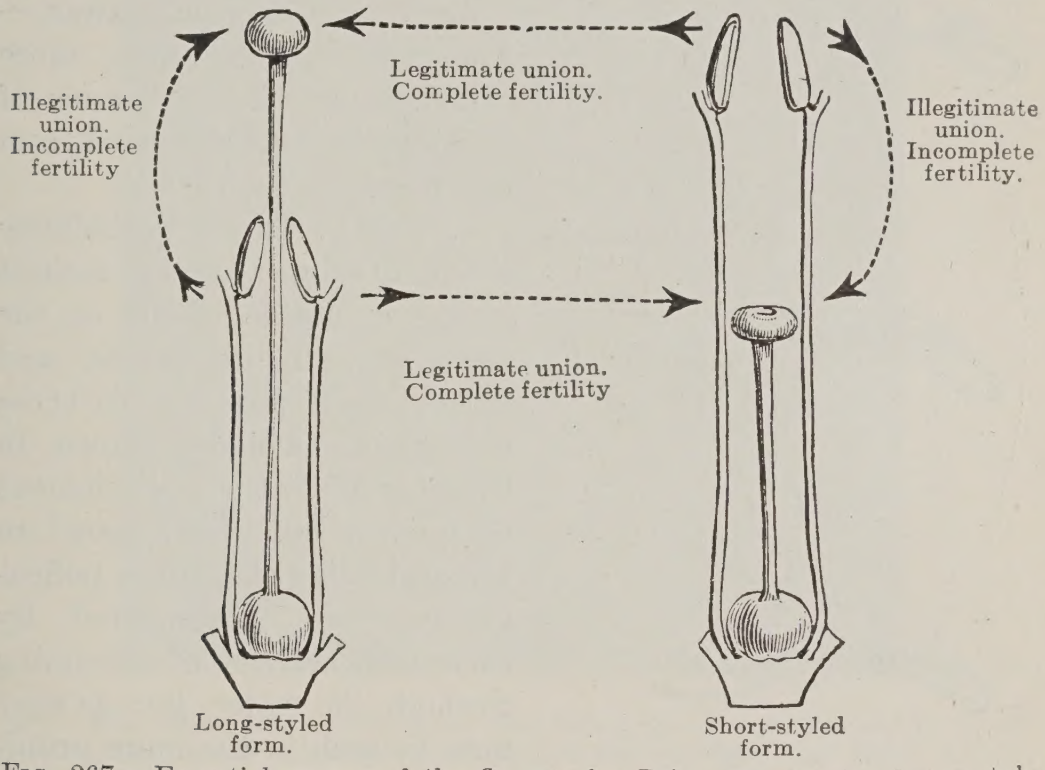


FIG. 267.—Essential organs of the flower of a Primrose, showing heterostyly and various possibilities of cross-pollination. (After Darwin.)

of the same flower; and if cross-fertilization fails, such self-fertilization will be advantageous to the plant, as it will thus be saved from complete barrenness."

There also exist heterostyled *trimorphic* plants, the three forms known respectively as *long-styled*, *mid-styled*, and *short-styled*. The Purple Loosestrife (*Lythrum Salicaria*) and the Pickerel-weed (*Pontederia cordata*), which grows along the margin of streams[1]

[1] The family Pontederiaceae are believed to contain the only heterostyled forms known among plants with one cotyledon. Other examples, from among dicotyledons, are other species of *Lythrum*, *Decodon verticillatus* (swamp loosestrife), and numerous species of the genus *Oxalis* (sorrel).

and ponds, may be cited as illustrations. (Fig. 268.) In this species the stigma of the long-styled form was found by Hazen to reach an average height of 12.5 mm. above the base of the ovary, while that of the short-styled form reached a height of 2.7–3 mm. The height of the stigma of the mid-styled form was found to be 7–8 mm. The pollen grains of the short-styled forms are much larger than those of the long-styled forms.

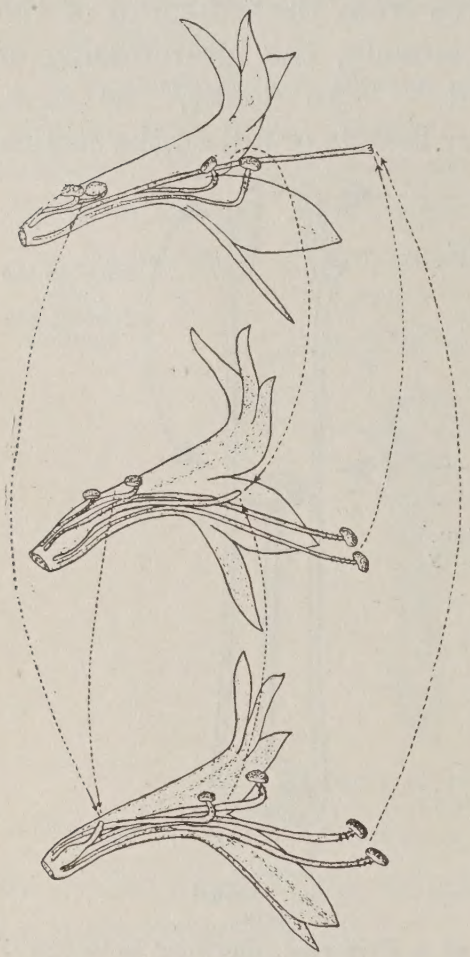


FIG. 268.—Flowers of Pickerel-weed (*Pontederia cordata*), showing Dimorphy. Above, a long-styled flower; center, medium-styled; below, short-styled. The dotted lines with arrows indicate the six "legitimate" pollinations. From each flower a portion has been cut away in order to show the position of the short stamens, with their inverted anthers, and the short pistil. (After Hazen.)

Agents of Cross-pollination.—The following are the more common agencies by means of which pollen is transported from one flower to another.

a. Water.—In all probability the plants that appeared earliest in the evolution of life on the earth grew in the water, and did not bear flowers. In these plants (as will be shown in Chapter XXI) the male element or *sperms*, which correspond to the fertilizing element in pollen-grains, were transported by their own activity of swimming through the water, just as may now be seen in the more primitive forms of plant life. After the evolution of land plants some of them reverted to the aquatic habit, just as, after the evolution of mammals, some of them—such as the whale, walrus, and seal—became aquatic. Such aquatic flowering plants had two principal choices as to method of cross-pollination: either to lift their flowers well above the water on long flower stalks and trust to wind

or insects to carry their pollen, or to produce their flowers at the surface of the water, and depend upon the currents of water. An interesting example of the former is the lace-leaf (*Aponogeton fenestralis*), which grows wholly submerged until flowering, when it lifts its flowers up into the air (Figs. 269–270). The water-buttercup (*Ranunculus aquatilis*) and species of

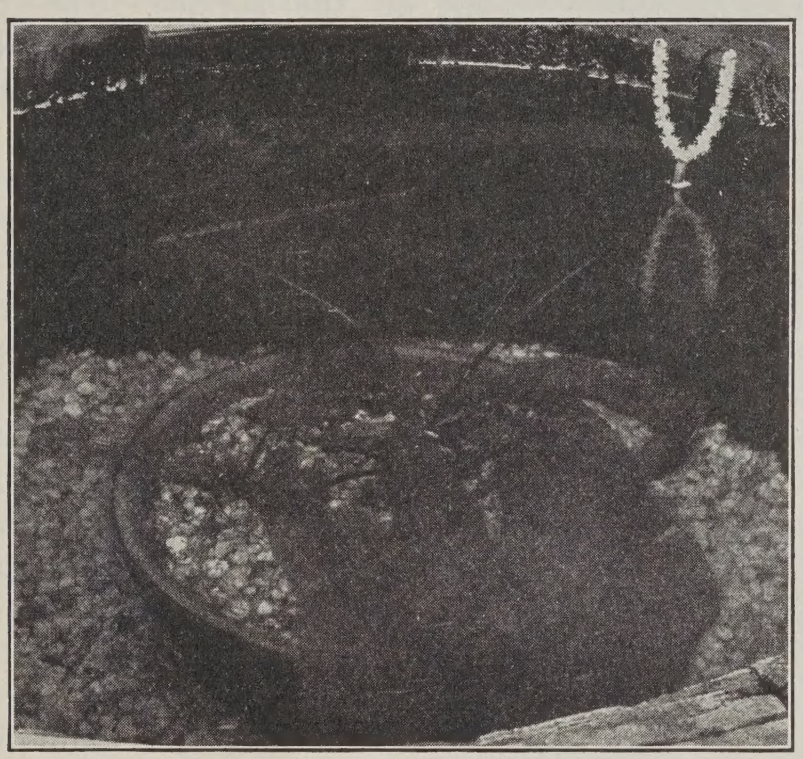


Fig. 269.—Lace Leaf (*Aponogeton fenestralis*), growing submerged in a tub of water, and lifting its inflorescence up into the air. (Cf. Fig. 270.) In the leaves of this plant the mesophyll develops only along the veins, leaving the spaces between the veins open, forming a lace-work, and thus helping to insure better illumination for all the leaves. The Latin specific name means "furnished with openings or windows."

Batrachium—also submerged, rooted aquatics—afford other illustrations of this habit. Their flowers are normally visited by different kinds of insects by which they are both crossed and selfed, but Hermann Müller states that, when the water is unusually high, the flowers of *Ranunculus aquatilis* remain submerged and unopened, pollinating themselves, as in normally cleistogamous species.

The Waterweed (*Elodea canadensis*) is a submerged floating aquatic, with some plants dioecious and some polygamous[1] (*i.e.*, it is *trioecious*). The staminate flowers, formed under water, separate from the plant when mature, and rise to the surface, buoyed up by the gases they give off. At the top of the water the pollen is discharged and floats on the surface. The pistillate flowers are lifted a little above the surface by the elongation of the calyx-tube, which is said to reach a length of from two inches to one foot. The flowers commonly lie over on one side on the water-surface, and the prominent, recurved stigmas, not easily wetted by water (because hairy), form a depression on the surface film. This tiny depression or "dimple" in the water surface facilitates the rapid and sure approach of the floating pollen-grains to contact with the pubescent (hairy) stigmas, to which they adhere.[2]

FIG. 270.—Inflorescence of the Lace Leaf. (Cf. Fig. 269.)

b. Wind.—The more primitive[3] land plants, such as the pines, hemlocks, spruces, and other gymnosperms, and the poplars, walnuts, birches, oaks, nettle, and hop, have relatively incon-

[1] *Polygamous, i.e.*, having some plants with staminate or pistillate, and some with perfect flowers.

[2] The details of pollination of *Elodea* were clearly worked out by Wylie, R. B. *The morphology of Elodea canadensis.* Bot. Gaz. **37**: 1–22. 1904. According to Wylie, in *Elodea iowensis* the staminate flower is raised to the surface by the elongation of its stalk.

[3] Called *primitive* because they are considered to be earlier developed and, therefore, more closely related to the aquatic ancestors of the land vegetation, and have their flowers more simply organized than those of such groups as sunflowers, or orchids, whi ch represent the groups most recently developed.

spicuous flowers, lacking a showy perianth, but characterized by a great abundance of dry, powdery pollen. They are usually monoecious or dioecious and, in contrast to insect-pollinated plants (p. 386), the stigmas when present are characterized by a large surface area (Fig. 271). Many of the more recently developed plants (among the monocotyledons), such as the grasses, sedges, cat-tails, and plantains, also have simply organized, inconspicuous flowers. In all of these groups pollination is accomplished by the wind. The plants are called *anemophilous* (wind loving).

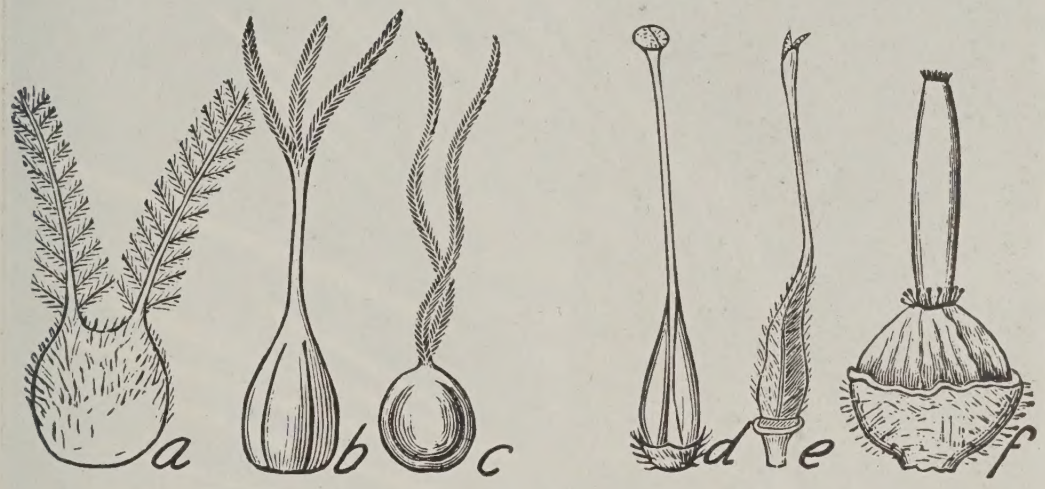


FIG. 271.—Pistils of various plants showing (*a-c*) stigmas of anemophilous and (*d-f*) of entomophilous flowers. *a*, long feathery stigmas of wheat; *b*, elongate hairy stigmas of a Rush (*Juncus*); *c*, long, hairy stigmas of Hemp; *d*, small capitate stigma of Tobacco; *e*, small two-lobed stigma of Digitalis; *f*, enlarged view of the small papillose stigma of *Centradenia floribunda*. (After Edson S. Bastin.)

Quantity of Pollen.—The chances of any given pollen-grain not reaching a stigma are so great that it is necessary for plants to produce an enormous quantity of pollen. Hassall,[1] who studied this question in 1842, referred to "the amazing number of pollen granules produced by most flowers." In a single blossom of the common dandelion (*Taraxacum*) he counted 243,000 pollen grains. "A flower of Paeony furnishes on an average 174 stamina, each containing 21,000 granules; these multiplied together give a total of 3,654,000; and in an entire Rhododendron

[1] Hassall, A. H. Observations on the structure of the pollen granule. Ann. Mag. Nat. Hist. **8**: 108. 1842.

plant the pollen grains amounted to the wonderful number of 72,620,000 . . . Great as these amounts are," said Hassall, "they sink into comparative insignificance when contrasted with the myriads produced by a single forest tree." Cat-tails (*Typha*) which bear an average of about 60,000 flowers on each spike, produce an enormous quantity of pollen; nearly one third of

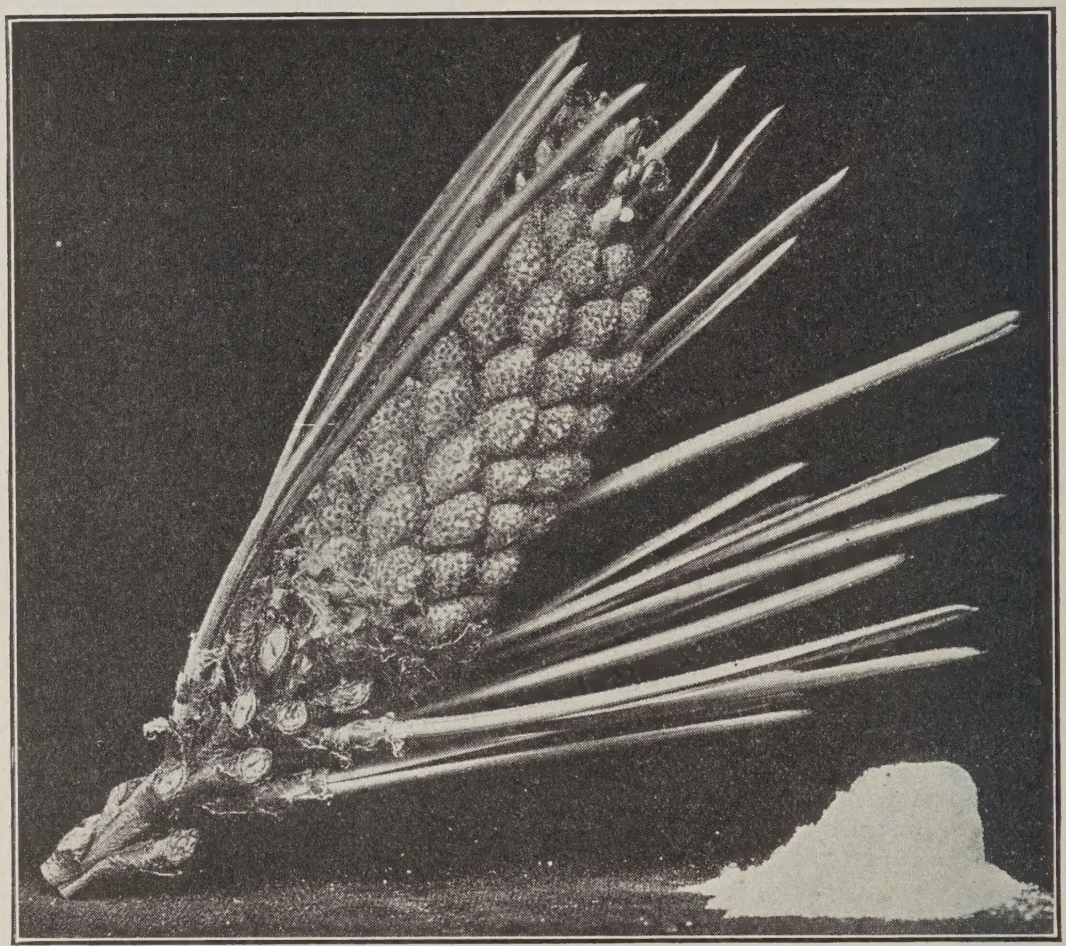


FIG. 272.—Branch of a Pine tree bearing numerous staminate cones and, at the right, a portion of the pollen grains shed from these cones and gathered into a pile. (After Leonard Bastin; Courtesy of *Country Life*.)

an ounce (144 grains by weight) was obtained in one case. Lazenby, investigating the ratio between the number of pollen grains and ovules in Indian corn, studied 5 varieties of dent, 4 of flint, and 4 of sweet corn. Dent was found to produce six times as many staminate as pistillate flowers, flint seven times as many, and sweet corn three and one half times as many. A medium

sized plant of maize has been found to produce as many as 50,000,000 pollen grains (*Cf.* Fig. 273). So much pollen of various anemophilous trees (not pines) fell in Troy, New York, in 1840 as to be plainly visible on all the flat roofs of the vicinity,[1] and Mr. H. Blake, of Boston, in 1842,[2] described a shower of pine pollen which fell on the deck of a vessel in Pictou harbor "on a serene night in June" so abundantly that it "was collected by the bucket full and thrown overboard." (*Cf.* Fig. 272; also, p. 402.)

Distance Carried.—When we recall that seeds of one of the pitcher plants (*Nepenthes ampullaria*) are known to have been blown by the wind from Ceylon to Seychelles, a distance of 1500 miles, and that inorganic dust is known to have been blown from Africa to Switzerland, we can easily understand that such very light and dry material as pollen may be carried great distances by wind. Thus, for example, Riley[3] states that, after a thunder storm in the middle of March, he "saw the ground in places in St. Louis sufficiently covered with pollen to appear as though sprinkled with sulphur; and this pollen, upon examination, proved by its trilobed and oily character, to belong to some pine, and probably to the long-leaved pine, which was at that time in bloom in the Southern States, and from which it must have been carried a distance of at least 400 miles. It is on record that a pistillate date-palm growing under cultivation near Otranto, Italy, set seed after having been barren for several years. The only known source of pollen was a staminate tree that grew at Brindisi over 40 miles northwest of Otranto, and which flowered that year. The pollen must have been borne that distance by the wind. Shamel observed pollen from a corn plant carried one half mile by wind, but in a corn field the pollen does not travel far, as it is intercepted by the thickly growing plants. Hesselman, who made observations in Scandinavia, collected pollen on prepared surfaces on two lightships, one 30 kilometers (18.6 miles) and the other 55 km. from shore. On board the latter ship he found pollen from spruce in the proportion of 408.9 grains

[1] Am. Jour. Sci. Arts **39**: 399. 1840.

[2] Am. Jour. Sci. Arts **42**: April, 1842.

[3] Riley, Charles V. Fifth Ann. Rept. on the insects, noxious, beneficial, and other insects, of the State of Missouri, p. 86. Jefferson City, 1873.

per square millimeter, and birch pollen in the proportion of 3649 grains per square millimeter.[1]

Structural and Other Adaptations.—In wind-pollinated plants the pollen is always abundant, always dry, often oily, of smooth surface, globular form, and, in some cases (*e.g.*, Pine), provided with tiny air-sacs which make it lighter and more buoyant (Fig. 303). Moreover, the anthers (in angiosperms) are often *versatile* (suspended at the middle), so that they move with great freedom and are thus shaken by the slightest breeze.

Often the anthers open in such a way that the pollen does not readily fall vertically downward, but is shed more or less laterally, and thus more readily carried away by the wind (Fig. 273). At the time for pollination hemlock cones hang pendent, the scales opening toward the earth so that the buoyant hemlock pollen may float upward between the cone-scales to the naked ovules.[2] The pollen-grains of wind-pollinated plants also *average* smaller in size than those of insect-pollinated plants, seldom exceeding 0.03–0.04 mm. in diameter, while the grains of entomophilous species average much larger, sometimes reaching a diameter of 0.25 mm., as in *Mirabilis Jalapa.*

Viability of Pollen.—It must not be inferred, however, that because pollen may be transported for great distances it will be able to germinate, even on a suitable stigma, at the end of a long journey, for it may be dried out, or become too old, or spoiled by water or by innumerable other vicissitudes it may encounter. But pollen normally transported by wind is more resistant to such dangers than pollen normally carried much shorter distances by insects. Nor is wind-borne pollen necessarily more viable than pollen carried (for shorter distances) by insects. Thus, according to experiments made by Pfundt (cited by A. P. Saunders), among the wind-pollinated members of the grass family, the pollen of Indian corn (*Zea Mays*) does not retain its power of

[1] As Hasselman points out (Meddel. Stat. Skogsförsöksanst. No. 16, pp. 27–60, 1919), these facts have a bearing on the interpretation of problems in fossil botany, for the finding of fossil pollen-grains in peat moors, as is often done, does not necessarily indicate the previous vegetation of the moors.

[2] Murrill, W. A. The development of the archegonium and fertilization in the hemlock spruce (*Tsuga canadensis* Carr.) Ann. Bot. **14**:583–607. Dec., 1900.

germination for more than one day; the same is true of the flat-stemmed Meadow-grass or English Bluegrass (*Poa compressa*).

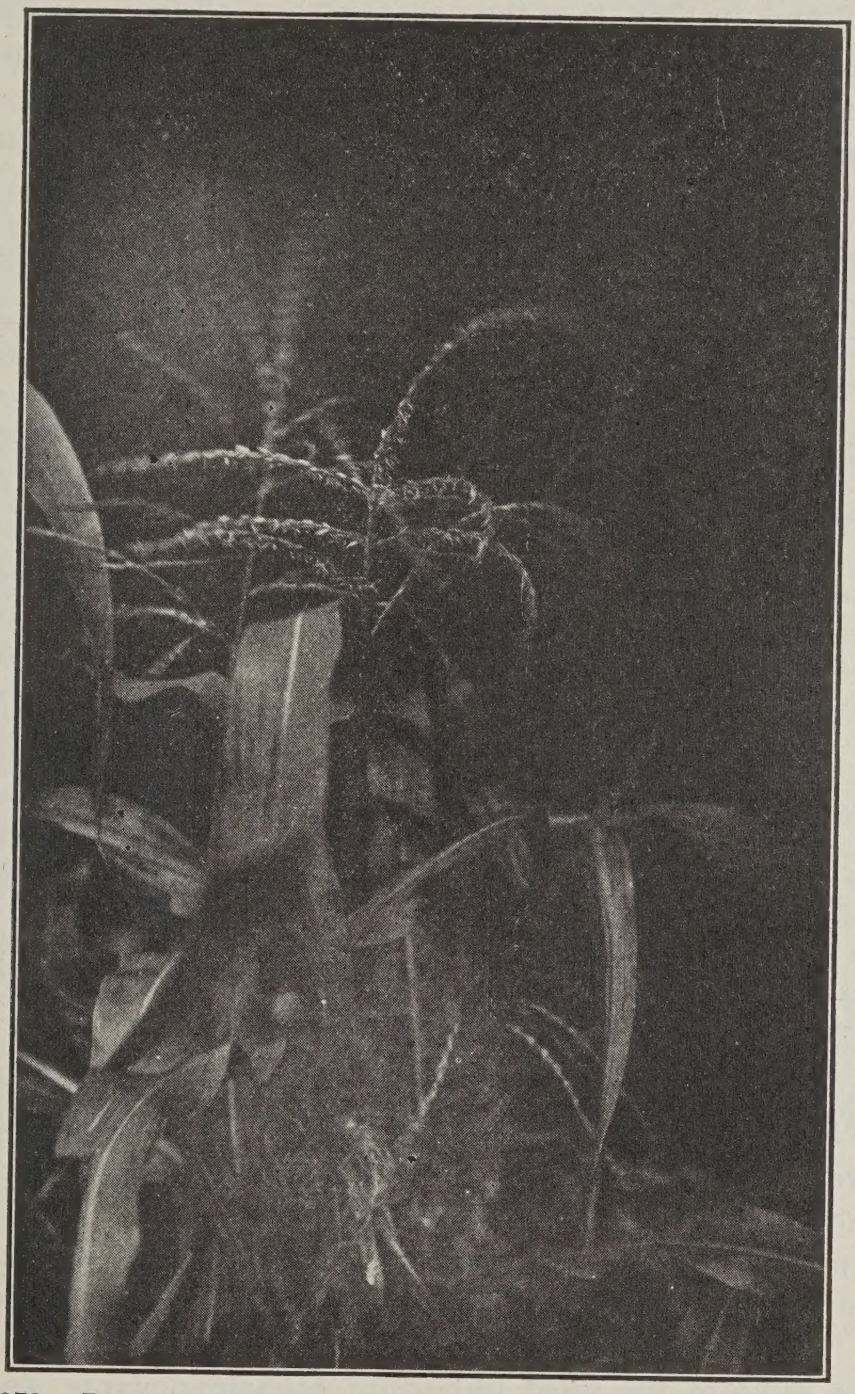


FIG. 273.—Portion of a plant of Indian Corn (*Zea Mays*), showing the cloud of pollen, dislodged from the "tassels" by gently shaking the plant in imitation of wind. The pollen was wafted away by a gentle breeze. (Cf. Fig. 307.)

The pollen of the insect-pollinated tomato, however, is known to remain viable for at least six months, and that of the grape for

about two months. Thoroughly dried carnation pollen may be kept viable for two weeks in closely stoppered bottles, and Kölreuter found, in 1766, that the pollen of the wall-flower (*Cheiranthus cheiri*) would retain its germinating and fertilizing power for 14 days.[1]

Saunders gives the following table of viability of various pollens under different conditions of humidity:

TABLE VII.—VIABILITY OF POLLEN UNDER DIFFERENT CONDITIONS OF HUMIDITY

Species	Number of days	
	Air dry	Zero humidity
Liliaceae		
Hemerocallis fulva	11	26
Tulipa Gesneriana	37	92
Iris graminea	20	57
Ranunculaceae		
Peonia albiflora	56	157
Trollius europaeus	29	124
Rosales		
Prunus avium	28	126
Lupinus perennis	129	164
Violaceae		
Viola odorata	35	235
Primula elatior	56	179

The pollen of peach and nectarine has been found to remain viable for from 9 to 22 days, apple 11–21 days, strawberry over 15 days, sweet pea 6 days in summer and about 23 days in winter, roses over 22 days, hybrid cannas 15 days.

c. Insects.—Insects are the most important of all known agencies for the transfer of pollen. Not only are more species dependent upon insects than upon any other agency, but these species include some of the most important economic plants, such as clover, alfalfa, beans, and other legumes; poppy, buckwheat,

[1] Much of the data on the viability of pollen is summarized by A. P. Saunders, in *The preservation of pollen for hybridizing.* Bull. Peony News No. 6. pp. 2–9. 1918. For viability of date pollen see p. 367.

apples, and many other fruit trees; currants, berries, beets, and numerous others. The subject has fascinated students of both plants and insects for over 200 years, and there is a large literature of popular and technical books and magazine articles dealing with the subject. It will be possible to give here only two or three striking examples.

The clover has already been mentioned in Chapter I. The flower of the bean (Fig. 274) is of the same type of structure (Leguminous or Papilionaceous) as the clover, and pollination is accomplished in a quite similar manner by means of the bumble-bee. It is recorded by Belt[1] that an early attempt to introduce scarlet-runner beans into Nicaragua failed because the right species of bumble-bee was not there. This recalls Sir Francis Darwin's remark that "the co-ordination between a flower and the particular insect which fertilizes it may be as delicate as that between a lock and its key."[2]

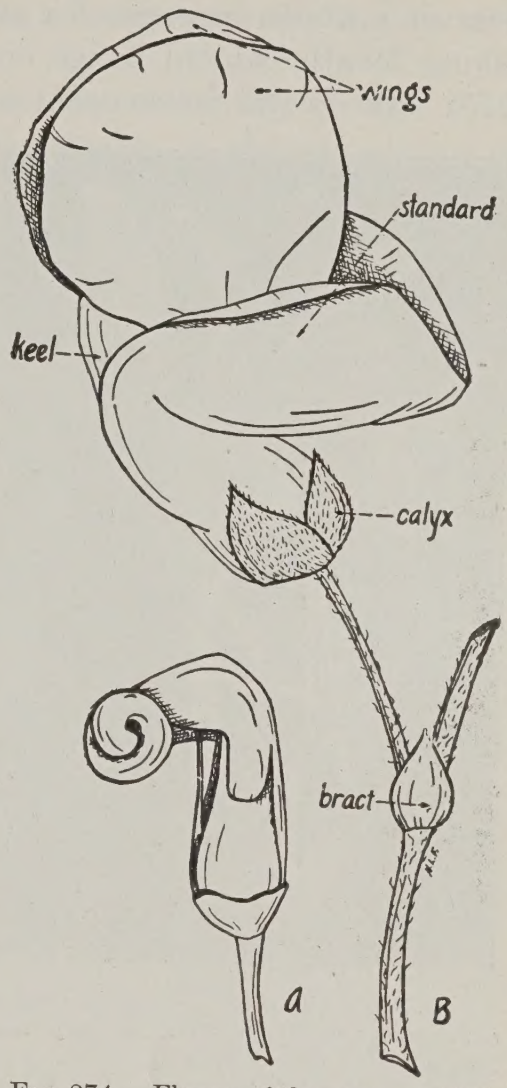


FIG. 274.—Flower of the common Kidney bean (*Phaseolus vulgaris*). A, spiral keel, enclosing the stamens and pistil (perianth removed); B, entire flower. (After Robbins.)

Perhaps the most wonderful and delicate adjustments of structure, function, and instinct to secure cross-pollination is found among the orchids. Darwin wrote to Sir Joseph Hooker,

[1] *Naturalist in Nicaragua*, p. 70. (Everyman's Lib. Ed., p. 56). This is of interest, for many, if not most of the Pea Family are self-pollinated; but Darwin and others (*Effects of Cross and Self Fertilization*, New York, 1877, pp. 168, 360) reported that the Scarlet Runner bean (*Phaseolus multiflorus*) sets few if any seeds when deprived of visits of bumble-bees.

[2] Darwin, Francis. *Life and letters of Charles Darwin.* Vol. 2, p. 436. New York, 1901.

"I never was more interested in any subject in my life than in this of orchids." There is room here for only one illustration, namely, *Angraecum sesquipedale*, of Madagascar. This orchid, in Darwin's words, possesses "a green, whip-like nectary of astonishing length [which] hangs down beneath the labellum (Fig. 275). In several flowers sent me by Mr. Bateman I found the nectaries eleven and a half inches long, with only the lower inch and a half filled with nectar. What can be the use, it may be asked, of a nectary of such disproportionate length? We shall, I think, see that the fertilization of the plant depends on this length, and on nectar being contained only within the lower attenuated extremity."[1] No moth with proboscis of sufficient length to reach this nectar was then known to science, but Darwin stated that there must be such a moth in Madagascar. It was subsequently discovered by W. A. Forbes (Nature 8 : 121. 1873).

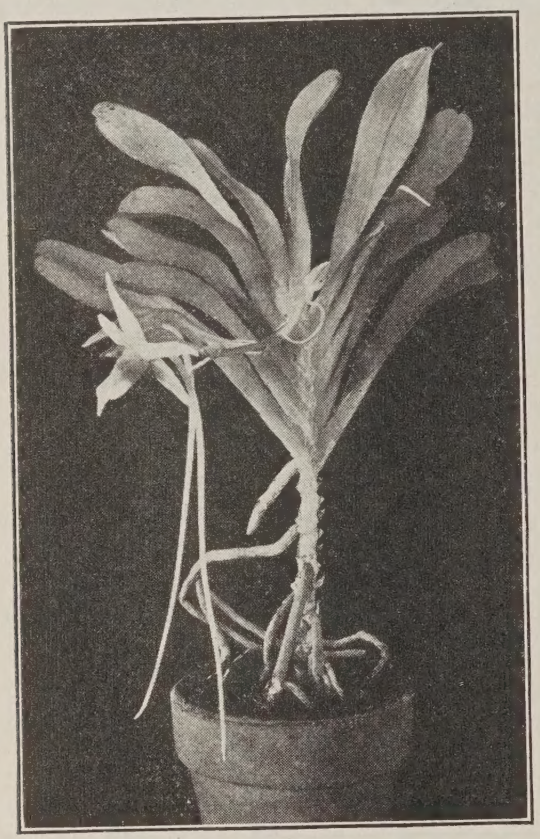


FIG. 275.—Plant of the orchid, *Angraecum sesquipedale*, with a nectary that measured 14 inches long.

There are various arrangements for insuring that the insect visiting a flower gets dusted with pollen. In some flowers he merely rubs against the open anthers when inserting his head for nectar. In the barberry (*Berberis*) the stamens are sensitive and snap forward when touched, throwing the pollen onto the insect; in the laurel (*Kalmia*) the anthers are imbedded in small pockets in the corolla, thus being bent over back when the flower is fully open (Fig. 276). When the corolla is slightly depressed, as by an insect lighting on it, the anthers are released and the stamen flies over in toward the center of the flower, throwing its pollen

[1] Darwin, C. On the fertilization of orchids by insects. pp. 162–163. New York, 1898.

onto the insect. In the milkweed the pollen masses (*pollinia*) are caught by the feet of the insect as he climbs over the flower, pulled out of their anthers, and thus carried to another flower (Figs. 277 and 278). Often the insects lose their legs in this process.

It is frequently stated that insects commonly confine their consecutive visits, during a given flight, to the same kind of

FIG. 276.—Flowers of Mountain Laurel (*Kalmia latifolia*). The anthers are retained in little pockets in the corolla so that the stamens are bent and held back as the flower opens. (Photo by Elsie M. Kittredge.)

flower. This would insure a more efficient transfer of the pollen than if the insects went from one species to another. Recent studies, however, show that we must generalize with caution in the matter of the constancy of insect visits to the same species. Clements and Long[1] have found that, at the end of the season,

[1] Clements, F. C. and Frances Long. Year Book, Carnegie Inst., Washington, No. 22. pp. 306–307. 1923.

constancy varies with the species of insect and with individuals, and especially with the weather.

The changing color of flowers from opening to fading also influences the visits of insects in some cases. Thus, to quote Clements and Long: "The various changes of color during anthesis in guiding bees to the flowers with abundant nectar is supported by studies of *Lotus* and *Lupinus*. One marked individual of *Bombus californicus* [a bumble-bee] paid 134 visits to the fresh yellow flowers of *Lotus glaber*, 4 to those [older] turning pale

Fig. 277.

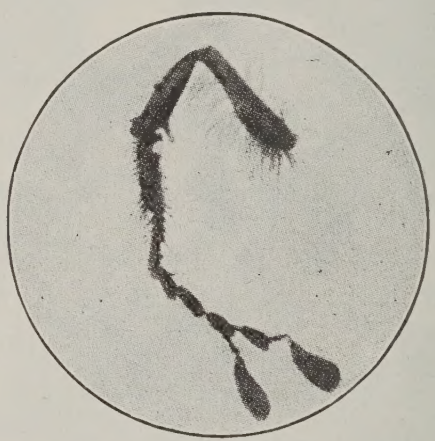


Fig. 278.

Fig. 277.—Photograph of a honey-bee gathering nectar from flowers of a milkweed (*Asclepias*). One leg is still fast in a stigmatic chamber of the flower last visited. Cf. Fig. 278. (After Stevens.)

Fig. 278.—Photomicrograph of a leg of a honey-bee with the remains of four pairs of pollinia clinging to it. One pollinium remains of each of the last two pairs, and only the *corpuscula* (the bodies to which the pollinia are attached) of the other two. The remaining six pollinia have probably been deposited by the bee in stigmatic chambers of flowers previously visited. (After Stevens.)

orange, and none to the old flowers which become orange-red. Another individual went to 250 fresh blue-purple flowers of *Lupinus affinis* without once heeding the older ones which were changing in color."

Shaw has demonstrated that beets are cross- and self-pollinated by *thrips*—species of Thysanoptera, so small as scarcely to be visible to the naked eye, the mature larvae measuring only $\frac{1}{27}$ inch long.

d. Other Agents of Pollination.—Among other agents for the transfer of pollen may be mentioned birds (Crown-imperial or

Fritillaria, and *Fuchsia* in New Zealand); humming birds (Darwin says that, in South Brazil, various species of Indian Mallow (*Abutilon*) set no seed without the aid of humming birds; in North America they visit the Touch-me-not—*Impatiens*); snails (wild Calla-lily—*Calla palustris*, and *Aspidistra*); and bats.

Cleistogamy.—Numerous plants possess, in addition to the showy "blossom," an inconspicuous flower that grows underground or close to the surface, and on which the plant chiefly relies for the formation of seed. These flowers never open, and are therefore dependent upon their own pollen (*cleistogamous*). Examples are the Violet (*Viola*), Peanut (*Hypogaea* Fig. 434), Touch-me-not (*Impatiens*), and the Milkwort (*Polygala polygama*), which bears its cleistogamous flowers in racemes on short underground branches or "runners." Asa Gray called attention to the great saving, in the plant's economy, of cleistogamy. The plant, in some cases, is spared the formation of an elaborate corolla, of nectaries and nectar, of color and odor, and the energy required in carpotropic movements. Moreover, there is an enormous saving in pollen. The number of pollen grains in the cleistogamous flowers of *Oxalis Acetosella* averages only about 400, of *Impatiens* 250, and in some violets only about 100, as compared with the thousands or millions (Peony) in entomophilous flowers, and the still greater number in those pollinated by wind.

Self-pollination.—In some of the most important agricultural crops, such as tobacco, wheat, barley, and oats, self-pollination is the rule. In wheat, barley, and oats the anthers discharge their pollen before the glumes open, thus insuring close-pollination and close-fertilization. Tobacco is chiefly selfed, the stigma being covered with the flower's own pollen before the flower opens. Honey bees and other insects come for nectar, and thus transfer pollen from one flower to another, and from one plant to another, resulting in a small percentage of crossing; but the flowers set seed perfectly well if covered with paper bags to exclude insects. Cotton is largely self-fertilized, but occasionally crossed. Bees visit the blossoms, to be sure, but they dust the stigma with pollen from its own flower as well as transfer pollen from one flower to another.

Insect Pollination and Plant Geography.—Nothing throws more light upon the course of evolution than data concerning the geographical distribution of plants and animals, and it is evident, at first thought, that the distribution of a plant species, normally dependent on insects for pollination, will be determined by the distribution of the given species of insect. Thus, for example, the northern limits of distribution of the genus *Aconitum* (Monkshood) in Asia is almost identical with that of the species of bumble-bee that pollinates it. The orchid, *Angraecum sesquipedale*, mentioned above, is not found outside of Madagascar, doubtless because the only insect that can pollinate it is indigenous to that island.

The alleged failure to introduce the scarlet runner bean (*Phaseolus multiflorus* Willdenow) into Nicaragua because of the absence there of the particular species of bumble bee on which this flower depends for cross-pollination, has just been noted (p. 387). The almost total lack of plants with showy blossoms in the Galapagos islands, in the Pacific Ocean, is correlated with a great scarcity of insects there. Describing the vegetation of the islands Darwin[1] says: "All the plants have a wretched, weedy appearance, and I did not see one beautiful flower," and later on he adds: "I took great pains in collecting insects, but excepting Tierra del Fuego, I never saw in this respect so poor a country." It may also be noted that dioecious species cannot spread as readily as monoecious and hermaphrodite species, especially if only staminate individuals are transported to the new locality.

Insect Pollination and Plant Evolution.—Bower[2] has called attention to the interesting correlation between cross-pollination (and the elaborate floral structures by which it is often secured) and the immobility imposed upon plants by growing rooted to one spot. This fixed position of all land-plants necessitates their dependence upon outside agencies for the transfer of their pollen, and is considered by Bower as the "prime factor leading to all those wonderful adaptations of the flower which have pollina-

[1] Darwin, Charles. Journal of researches (Naturalist's voyage around the world). New Ed. pp. 376, 387. New York, 1902.

[2] Bower, F. O. Plant-life on land. Cambridge, 1911.

tion as their end." The rocks of the carboniferous age contain fossil remains of dioecious plants, in which, strange as it may seem, fossilized pollen-grains are found on the carpellate or seed-bearing flowers. From this we know that cross-pollination took place, but whether by wind or by insects is not always clearly evident. However, what Bower calls "the outburst of evolution of flowering plants" took place during the geological period when the Mesozoic rocks were being laid down, and it is in the same rocks that we find the first abundant evidence of insect-life. This rooted habit of flowering plants is also considered by Bower to underlie the evolution of perfect (*i.e.*, hermaphrodite) flowers, for hermaphroditism insured self-pollination, and plants having this form of "insurance" would have their chances of producing seeds, and therefore of survival (in the struggle for existence), greatly enhanced.

CROSS-POLLINATION AND HORTICULTURAL PRACTICE

a. Growing Fruits under Glass.—In the forcing of such fruits (or vegetables) as tomatoes, under glass in cold weather, success rests upon proper pollination. When tomatoes, for example, are grown in the open the flowers are pollinated by bees and other insects, but under glass, in winter, the insects are not present, and hand-pollination must be resorted to. Nor is it sufficient to know that pollen must be transferred by hand; one must know how to apply it to the stigma in order to secure the best results. The setting of fruit in the tomato depends largely upon the fertilization of the ovules and the resulting formation of seeds. If the pollen is applied to only one side of the stigma the chances are that only the ovules on the corresponding side of the ovary will get fertilized; the result will be a poorly developed, or one sided fruit. When the pollen is evenly applied to the entire surface of the stigma the fruit is larger and more symmetrical, with seeds in each of its cells (Fig. 279). A successful method of transferring the pollen is to knock it out of the anthers into a spoon or other convenient receptacle, and then dip the stigmas of other flowers into it. It is not essential that a stigma be pollinated with pollen from the same variety, for Munson, by careful experiments at the State Agricultural Experiment Station of Maine (1898), found that

foreign pollen of tomatoes, while stimulating the development of the fruit, did not produce any immediate undesirable effect.[1] For example, the large Lorillard tomato crossed by the small "Currant" tomato gave, uniformly, fruit that was "in every respect typical of Lorillard."

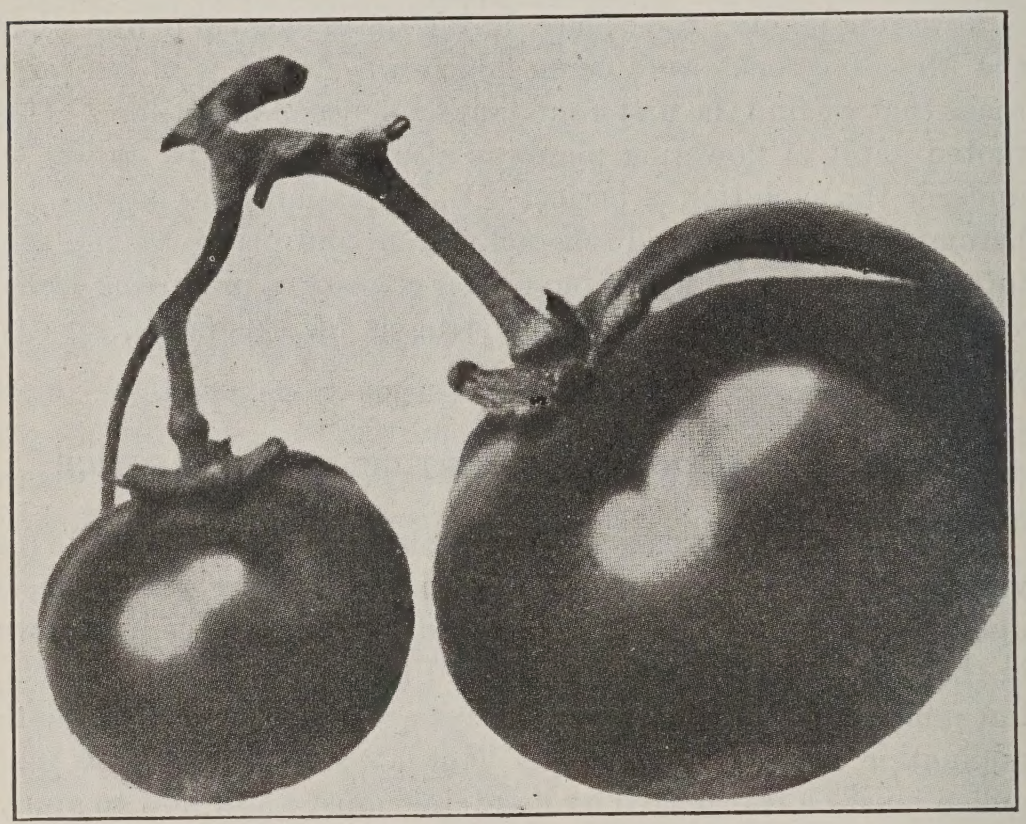


FIG. 279.—Two fruits of a tomato (*Lycopersicum*). The larger fruit developed from a flower that had pollen artificially applied so as to cover evenly the entire surface of the stigma. The smaller fruit developed from an adjacent flower which had much less pollen applied to its stigma. (After Munson. Maine Agr. Exp. Sta. 14th Ann. Rept.)

b. Successful Orchard Crops.—The failure of orchard crops is not always due to the same cause, but one of the causes is often imperfect or improper pollination. Some orchard fruits are *self-fertile*, while others are wholly or in part *self-sterile*. Tests of various orchard fruits and small fruits have yielded the following information:

[1] Nor on the fruits of other plants of the same family (Solanaceae), such as egg-plant, nor on Cucurbits (cucumber and melon).

Self-fertile

Grapes (Concord, Niagara, Delaware, and six others).
Currants (red and white).
Gooseberry.

Self-sterile (wholly or in part)

Grapes (Merrimac, and 13 other varieties).
Pears (Bartlett, Kieffer, Flemish Beauty, Seckel, and others).
Apples (Bellflower, Spitzenberg, Winesap, and most others).
Plums (most varieties of native plums, and many others).
Cherries (most varieties).
Peaches, Apricot, Prune, Olive.

It is instructive for us to realize that this knowledge has been obtained by the most painstaking and laborious experimenting and observation, and represents the results of studies by many observers, extending over hundreds of years. The most thorough and systematic work has been done during the past 25 or 30 years. Lewis and Vincent, for example, at the Oregon Experiment Station (1909), studied 89 varieties of apple, finding 59 self-sterile, 13 partly self-sterile, and 15 self-fertile.

FIG. 280.—Honey-bee visiting a flower of the pear (*Pyrus*). Cross-pollination of pears is accomplished almost wholly by insects. (After Fletcher. Virginia Polytechnic Inst. Agr. Exp. Station.)

In his studies of sterility in the plum, Waugh, at the Vermont Experiment Station (1897), protected 6365 blossoms from cross-pollination and found that only 3 of them set fruit. Fletcher's conclusions as to the sterility of pears are based on the results of hand-pollinating 8408 Kieffer pear blossoms, and 9867 blossoms of the Bartlett pear. These experiments, conducted at the Virginia Experiment Station, extended over three years (1903, 1906, 1907).

The yield of plums is often greatly diminished by what is known as *June drop*. Since nearly half (41%) of the fallen fruit studied by Waugh (Vermont Station, 1899) had not been ferti-

lized, he concludes that this failure is one of the chief causes of the trouble.

c. Remedy for Failure of Orchard Crops.—Where failure of orchard crops is due to lack of proper cross-pollination, the remedy is evidently to be found in any measures that will tend to insure crossing. Fletcher found that the labor of hand pollinating insured a much larger crop of pears, but this is a very laborious

FIG. 281.—Comparative size of cross-pollinated (left) and self-pollinated (right) Kieffer pears. (After Fletcher. Virginia Polytechnic Inst. Agr. Exp. Station.)

process, and might become too expensive or otherwise impracticable.

In the case of fruits dependent (as most of them are) upon insects for cross-pollination, Waite and others have recommended keeping a hive of bees in the vicinity of the orchard (*Cf.* Figs. 280 and 281). In order to test the efficacy of neighboring bees Hendrickson[1] covered two pairs of French and Imperial prune

[1] Hendrickson, A. H. The common honey bee as an agent in prune pollination. California Agr. Exp. Sta. Bull. 274. Dec., 1916.

trees with tents made of mosquito netting. Both tents were completed before any blossoms opened on the trees, and were made as nearly insect-proof as possible. As soon as 25% of the blossoms had opened a hive of honey bees was placed under one tent and kept there through the blossoming period, which lasted about five days. All bees and other insects that might carry pollen from one blossom to another were carefully excluded from the second tent. After blossoming was over both tents were taken down.

The bees seemed to prefer the flowers of the French prune, and the tree of this variety, under the tent with the bees, set a much

FIG. 282.—Bee hives placed in a plum orchard to insure cross-pollination by the visits of the bees from flower to flower. (After Kinman, U. S. Dept. Agr. Farmers Bull. No. 1372.)

heavier crop of fruit than that of the best fruited tree exposed to normal conditions. The crop was so heavy that the limbs had to be propped up to prevent their breaking with the weight of fruit. On the other hand the French prune tree under the tent from which bees and other insects had been excluded set a very light crop. Kinman[1] states that the presence of bees in the plum orchard is almost an economic necessity (Fig. 282). The visits of insects are favored by sheltered situations and windbreaks.

It is also recommended to plant mixed orchards, or at least to avoid planting blocks of one variety. Coats[2] observed that a

[1] U. S. Dept. Agr. Farmers' Bull. 1372. Aug., 1924.

[2] Coats, L. Pollination of plants. California Fruit Grower **20**:6. 1897.

block of 500 six-year-old d'Agen prune trees all blossomed well but fruited very poorly, except one row which stood next to a row of "Grand Duke" plums. The trees in that row fruited well, for plum pollen is effective on the stigmas of prunes, the latter being a special type of plum.[1]

In planting mixed orchards it must be kept in mind that cross-pollination does not result by transferring pollen from one tree to another of the same grafted variety; such trees, though growing independently on their own roots, represent, in effect, the same individual. It is necessary to use pollen from a tree of a distinct (and suitable) variety—that is, one produced from a different seed. Where blocks of trees of the same variety are already established, the yield may be increased by grafting on each tree scions of other varieties as a source of foreign pollen.

In planning the orchard so as to insure cross-pollination it is necessary to know the times of flowering of the various varieties. The exact date varies, of course, with the locality, but varieties generally maintain the same sequence and overlap, some being early and some late bloomers. Lists of the varieties of apples and pears, arranged in order of flowering, have been published in horticultural journals. In some places it is customary to plant an orchard with only about four rows of trees of the same variety side by side, then one or more rows of another variety whose flowering period overlaps that of the first variety, and so on throughout the orchard.

d. Deterioration of Cotton.—In most of the cotton-growing communities of the United States good varieties are, within a few seasons, replaced by inferior mixed stocks, resulting in loss of yield and in fiber of poor quality. This is caused in large part by growing several varieties in adjacent fields. The seed becomes

[1] The European or domestic plum and the prune belong to the same species (*Prunus domestica*). The fruit is handled differently depending upon the use to which it is to be put. The use of the words "plum" and "prune" dates back for several centuries. The word "plum" comes from the Latin (*prunum*) through the Anglo-Saxon word *plume*, while "prune" comes to us from the Latin through the French word *prune*. Any plum fruits which may be dried sweet with the pits in and without fermenting may be converted into prunes. Most plums ferment in the process of being so treated. Some plums are dried after the pits are removed and are then not called prunes but dried plums.

mixed in public gins, and in the next crop cross-pollination occurs extensively, resulting in inferior seed and the gradual establishment of degenerate stocks. As the most effective remedy for this evil the U. S. Department of Agriculture recommends that only one variety be grown in a given community; this will forestall the mixing of seed and subsequent deterioration through cross-pollination.[1]

e. Selective Pollination of Cotton.—When different varieties or even different species (Upland and Egyptian) of cotton grow near together so that both cross- and self-pollination take place, most of the ovules (about 75%) are self-fertilized, even when there is complete compatibility between the different species when only one kind of pollen reaches the stigmas. This is called *selective fertilization.* Observations of Kearney and Harrison[2] show that there is generally on a stigma a majority of pollen grains from the same flower, even though the flower is admirably adapted to cross-pollination. The percentage of foreign pollen is greater for Upland cotton than for Egyptian. Kearney and Harrison suggest the hypothesis that, in some way not yet understood, the presence of like pollen prevents the germination or subsequent development of many of the foreign pollen-grains where both kinds are present on the stigma. It would appear that the inhibiting factor does not reside in the stigma itself for, when applied separately, foreign pollen is not inferior to like pollen in rapidity of growth and ability to bring about fertilization.

f. Storage and Shipment of Pollen.—It often becomes desirable to store pollen for use at a later date, or to ship it for use at a distant point. Thus, for example, we have noted above the process of forcing tomatoes under glass in winter. It has been found desirable, at times, and quite possible, to store pollen, gathered in the fall from the plant intended to serve as the male parent, for as long as six months. In the case of most pollens, satisfactory storage depends upon keeping them dry. The method employed by Simon, in Europe, was to place the pollen in a small container

[1] Cook, O. F. One-variety cotton communities. U. S. Dept. Agr. Bull. No. 1111. Nov. 25, 1922.

[2] Kearney, Thomas H. and George J. Harrison. Selective fertilization in cotton. Jour. Agr. Res. **27**: 329–340. Feb. 9, 1924.

plugged with cotton; this is placed in a larger vessel, also covered with cotton and containing water-free calcium chloride, which absorbs water vapor from the air. By this device Simon was able to keep pumpkin pollen 5 weeks, and Rhododendron (Kohinoor) pollen 13 weeks.

Green used quinine capsules for gathering and storing pollen. He found that the pollen of a number of fruits adheres to the walls of the capsule, from which it may be transferred to the stigmas by a small brush. Pollen so enclosed was found to remain viable for "a long time," and could thus be shipped to considerable distances, if desired. The pollen of certain tropical plants is commonly distributed through the West Indies on dry blotting paper, enclosed in pasteboard boxes. In this way it will keep for three weeks.

During 1902 the Central Experiment Station at Ames, Iowa, secured pollen from Missouri for cross-breeding experiments with various kinds of fruit trees; from Ames it was distributed to other stations and individuals.[1] The well known case of storing the pollen of dates for a year or more in classical times—especially during periods of war—has been referred to on page 367. The chief source of danger to guard against is moisture, which is injurious, not only directly, but indirectly by favoring the growth of mildew on the pollen. The pollen of the garden nasturtium (*Tropaeolum majus*) is specially sensitive to water. It has been found that this pollen, if not wetted, will keep in artificially dried air for 88 days, while, if wetted for only two minutes, and then placed in artificially dried air, it retains its vitality for only two days. The longer the wetting, the more disastrous the result. Each pollen-grain of most plants is protected against being easily wetted by a delicate surface-coating of oil. Many flowers have more or less elaborate provision, in structure or otherwise, against the wetting of their pollen. The closing of many flowers (such as dandelion) on cloudy and rainy days, and at night when dew falls, thus serves to protect the pollen. In addition to its directly injurious effect, rain may also prevent the scattering of the pollen until the stigmas have

[1] Price, H. C. Report of the Central Station at Ames. Rept Iowa State Hort. Soc. **37**: 220. 1903.

ceased to be receptive. This is often a factor in diminishing the yield of orchard- and other fruits. In contrast to *Tropaeolum* there may be mentioned an undetermined species of *Abutilon* whose pollen kept best at a relative humidity of 60 to 90 per cent.

Pollination and Legislation.—Experiments of Panton, in Canada, showed that the spraying of plants with Paris green injured both the bees and the fruit directly, thus diminishing the yield. In recognition of this fact, the Legislature of Ontario, in April, 1892, enacted a law forbidding the spraying of fruit trees during the blooming period with "any mixture containing Paris green or any other poisonous substance injurious to bees."

Pollen and Hay Fever.—Hay fever, or bronchial asthma, was first described as a disease, distinct from an ordinary "cold in the head," in 1819, and attributed to irritation by dust, but pollen was not thought of as a possible cause until 1873, when Blackley demonstrated that pollen-grains were common in ordinary air; he artificially induced hay fever symptoms by having patients inhale air containing pollen-grains. Like most new ideas, the theory that pollen is a cause of hay fever was only slowly and reluctantly accepted. It is now generally known, not only that pollen is a cause, and probably the chief cause of the disease, but that individuals may be immune to certain kinds of pollen while at the same time highly susceptible to other kinds. This accounts for the seasonal recurrence of the affliction. Only about one per cent. (1,000,000) of the population of the United States are susceptible to the disease from any cause.

The plants whose pollen is the chief offender in this matter are mostly weeds, which Scheppergrell[1] calls the "parasites of agriculture." The most important are the Ragweeds (*Ambrosia artemisiifolia* in particular, *A. trifida*, and others), Wormwoods (*Artemisia*), Russian Thistle (*Salsola*), Pigweeds (*Amaranthus* sp.), Yellow Dock (*Rumex crispus*) and other weeds; many grasses, including corn, wheat, oats, timothy, Buffalo grass (*Buchloe dactyloides*), and numerous trees, including practically all species of Oak (*Quercus*), Cedar (*Juniperus*), Black Walnut (*Juglans nigra*), Poplars (*Populus*), and Elms (*Ulmus*).

[1] Scheppergrell, William. Hay fever and asthma. New York, 1922. The information given above on this subject is based on this work.

In general, plants whose pollen is likely to cause hay fever are confined to wind-pollinated species. They usually have inconspicuous flowers, and bear enormous quantities. Contrary to the general belief, the Goldenrods (*Solidago*), Roses (*Rosa*), White Daisy (*Chrysanthemum leucanthemum*), Dandelion (*Taraxacum*), Clovers (*Trifolium*), and several other plants having a bad reputation in this respect, are all pollinated by insects. Their pollen is never found in the air, and in all probability they never cause hay fever, or are at least negligible factors. "Rose cold" is, therefore, not caused by roses.

The amount of pollen given off by the plants that cause hay fever is really enormous. According to Scheppergrell one flower of a Feverfew (*Chrysanthemum Parthenium*) gave off 22,916 pollen grains in twenty-four hours. A large specimen of this plant bore 9902 flowers, giving a total of 227,000,000 pollen grains in one day. It was calculated that between 8 a.m. and 1 p.m., on a certain day, there were given off from a single plant of *Ambrosia trifida* the amazing number of eight thousand million (8,000,000,000) pollen grains. It has been found experimentally that the rough pollen grains of this Ragweed will travel one-half mile in a wind of 20 miles per hour over level ground, and many times as far when lifted by upward currents. The smooth pollen of grasses will travel only 456 feet under similar circumstances. These things, combined with the great quantity of pollen, account for the fact that the Ragweed is the very worst offender in hay fever. (*Cf.*, also, p. 381.)

By an apparatus known as the anemophilometer (designed in the laboratory of the American Hayfever Prevention Association, New Orleans) studies have been made of the number of pollen grains floating in the air. Flowers are placed in an artificial "wind" of known velocity produced by this apparatus, and the dislodged pollen grains are caught on a microscope-slide coated with glycerine or other sticky substance. They may then be counted under the microscope. By this means it has been shown that a wind that will carry pollen of the common Ragweed one half mile will carry the pollen of Corn (*Zea Mays*) only 43 feet. Information obtained by the use of this apparatus may also be applied in studying the probability of the chance cross-pollina-

tion of various wind-pollinated cultivated plants, when grown at specified distances apart.

Scheppergrell states that, by exposing "pollen plates" similarly prepared, it was found that, on a certain day in October, 1920, there were 61 pollen grains of the common ragweed per square yard of air at New Orleans. It has also been found that this pollen, "under favorable wind conditions, will traverse a distance of five miles in sufficient numbers to cause hay fever." It has also been shown that this pollen will not travel as far as fifteen miles in quantities sufficient to cause the disease.

Bronchial asthma, when caused by pollen, is known as *pollinosis*. When the attack occurs in the summer and fall it is commonly called "hay fever;" when it occurs in the spring it is often called "rose cold." Until recently it has been generally believed that hay fever, in all its various forms and seasons, was an incurable affliction, to be relieved (but not cured) only by change of climate, but, through the studies of Dr. I. Chandler Walker, of the Peter Bent Brigham Hospital (Boston), and others, it has now been established that bronchial asthma is frequently (if not always) due to the fact that the sufferer is "sensitive" or anaphylactic[1] to some form of protein, which is the cause of the trouble. With proper treatment, now well known, most sufferers may be either cured or greatly benefited.

The theory, now well established by clinical practice, is that the respiratory tract is sensitive to (*i.e.*, easily irritated by) some form of protein. The patient may be sensitive to one or more proteins. To use the words of Walker,[2] bakers frequently have bronchial asthma from the inhalation of the flour with which they work. A man whose work consisted of sifting green coffee beans became sensitized to the protein in the green husks and had asthma from the protein. Attacks of asthma which occur only

[1] *Anaphylaxis* means "increased susceptibility to an infection or to the action of a foreign protein introduced into the body following a primary infection; the opposite of immunity" (Stedman's Med. Dict.). The word is from the Greek word φύλαξις, *phylaxis* (*security*), with the prefix ἀνά, *ana* (*again*), with the sense of increase. The same Greek word appears in *prophylaxis*, meaning preventive or protective treatment.

[2] Walker, I. C. A clinical study of 400 patients with bronchial asthma. Boston Med. Surg. Jour. **1918**: 179, 288. 1918. I have freely followed Walker's phraseology without using quotes.

during summer months are usually caused by the pollen of plants, but the irritation is not due to the germination of the pollen-grains on the mucous membrane, as was formerly thought. In many instances this summer type of pollen asthma is prolonged throughout the year by bacteria which, because of the patient's lowered resistance, cause a bronchitis, and this in turn causes asthma. In a few cases the early type of a summer asthma is due to bacteria and not to pollen.

The various forms of proteins may enter the body either by *inhalation* (pollen, animal hair and dandruff, flour of different cereals, "dust," etc.); or by ingestion (various protein foods); or by *absorption* which, apart from inhalation and ingestion, concerns the conjunctiva and, to a less extent, the skin; or by *infection*, especially by bacteria in certain well known *foci of infection*, such as the teeth, tonsils, nose, throat, and lungs. This action of bacteria is apart from their infectious action in causing a specific bacterial disease. Some persons appear to be sensitive to their own secretions.

In order to test a patient to ascertain whether he is protein-sensitive and, if so, to what specific protein, a number of small cuts, about one-eighth of an inch long, are made on the surface of the forearm. These cuts are not to be made deep enough to draw blood. On each cut is placed a protein suitably dissolved to facilitate its rapid absorption. At the end of half an hour the proteins are washed off and the reactions are noted, always comparing the inoculated cuts with normal controls on which no protein was placed. If the patient is sensitive to a given protein the cut area to which that protein was applied will show a white elevation or resemble the effect of the stinging nettle. This is called a "positive" reaction. Negative reactions show that the given proteins are not a cause of asthma in the patient under test. Bacteria, however, though giving a negative skin test, may be a cause of asthma through their infectious nature. The tests should never be attempted except by a competent physician.

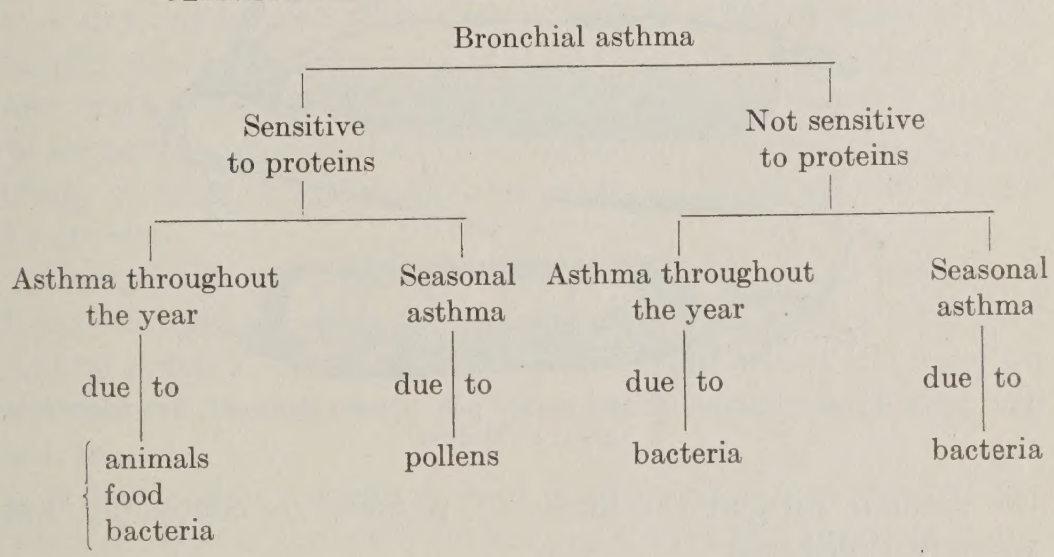
If the patient is found to be sensitive to food proteins such foods should be omitted from the patient's diet, at least temporarily. Patients sensitive to bacterial proteins may be desensitized by hypodermic injection with the vaccines of those organisms; when

pollen is the cause of the positive reaction, treatment by injection of extracts of the given pollen is indicated.

Walker cites the case of one patient who had had continuous bronchial asthma for sixteen years, beginning at the age of 18 months, and who proved to be very sensitive to wheat proteins; the omission of wheat from her diet relieved the asthmatic condition. In another case the patient was confined to his bed from August to April with "hay fever" caused by ragweed pollen. He showed skin reactions to both ragweed and feather proteins. That is, "ragweed put the patient to bed and the feather pillow kept him there." He was promptly relieved by removal of the feather pillow, and was then desensitized by treatment with ragweed-pollen extract.

Walker has tabulated the causes of bronchial asthma as follows: (*The Doctor's Factotum* **12**: 48. April, 1919.)

CLASSIFICATION OF CAUSES OF BRONCHIAL ASTHMA



Proteins for cutaneous tests are now available for about 100 foods, 12 bacteria, 8 epidermal proteins (hair of various animals, horse dandruff, sheep wool, feathers), and about 50 different kinds of pollen including that of various trees, cultivated plants, grasses, and various weeds, including the Ragweeds, various Goldenrods, Daisy, Rose (*Rosa rugosa*), Clover, Dandelion, Corn (*Zea Mays*) and others.

CHAPTER XVIII

KINDS AND CLASSIFICATION OF FRUIT

The word fruit is commonly used to designate the mature, edible product of a flower, but outside of scientific discussion the term is loosely used. Numerous fruits (botanically speaking), such as, tomatoes, squash, egg-plant, and others, are commonly called not fruits but "vegetables," while other fruits, such as the corn grain and other cereal grains, and the corresponding parts of the maple, elm, dandelion, and various other plants, are usually called "seeds." Some true seeds, such for example as

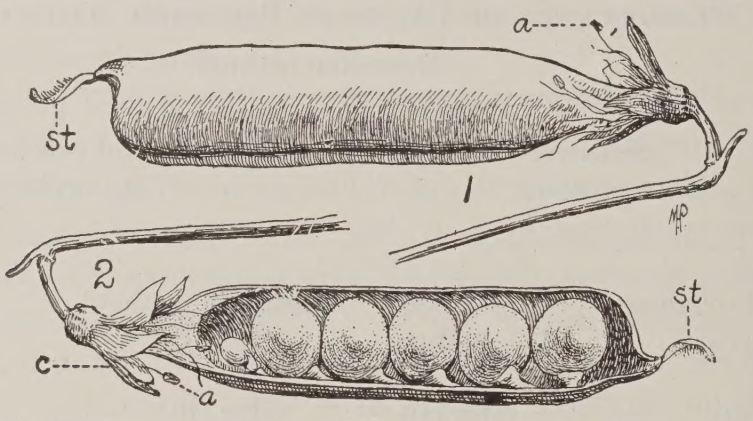


FIG. 283.—Fruit (legume) of the edible pea (*Pisum sativum*). *a*, anther; *c*, calyx; *st*, stigma.

the coconut without the husk (*Cf.* p. 859), are commonly, but wrongly, called fruit.

Simple Fruit.—Botanically speaking *a fruit is a ripened ovary*, together with any adjacent structure closely united with it. A ripened ovary without any adjacent structure is a *simple* fruit. In a simple fruit the ovary wall is called *pericarp*, within which are the ripened ovules or seeds. The pea pod is an excellent illustration of a simple fruit. An examination of figure 283 (or, better still, of an actual specimen), in comparison with a pistil of a pea flower, will enable one readily to identify the enlarged ovary or pod, containing the seeds or "peas." The stem of

the pod is the peduncle of the flower, and the shrivelled calyx usually persists at the base of the pod. At the opposite end or tip of the pod is the persistent, but wilted, style.

When simple fruits open spontaneously at maturity they are called *dehiscent;* when they do not they are *indehiscent.* The term "pod" is applied to the various kinds of dehiscent fruits, as follows:

Legume, a pod dehiscent along both sutures (bean). Some legumes, as in the clover, do not dehisce, and in certain species of Leguminosae the fruit closely resembles an achene. In the bush clovers (*Lespedeza*) the legume breaks up into one-seeded segments. Sugh a legume is called a *loment.*

Follicle, a pod that dehisces along one suture only. Larkspur, milkweed, magnolia (a fleshy follicle).

Capsule, a pod formed from a compound pistil (Iris). A two valved capsule, as in the radish, mustard, and other plants of the same family (Cruciferae), is a *silique.*

A dry indehiscent fruit with a wing is a *key* or *samara* (ash, maple, elm); when the wing is absent, but the fruit small, hard, and one-seeded we have an *achene* (or akene). A *nut* is similar to an achene, except that it is larger, and is developed from an ovary of more than one cell and ovule, of which all but one fail to develop.

Fleshy fruits are obviously indehiscent. When the pericarp is fleshy throughout (tomato, banana, grape) we have a *berry.* It will be noted at once that most of the fruits called "berries" in the market (except, *e.g.,* the gooseberry) are, botanically, not berries.

A berry with a leathery rind (orange) is a *hesperidium;* but when the rind is derived from the calyx, as in the watermelon and other cucurbits, the fruit is called a *pepo* or *gourd.*

When the fruit is fleshy throughout, but derived largely from parts adjacent to the pistil (calyx, receptacle, etc.), as in the quince and apple, we have a *pome.*

In the *drupe,* or "stone fruit," the inner layer (*endocarp*) is hard and stony, enclosing the seed; the next outer layer (*mesocarp*) is juicy or succulent, *e.g.,* walnut, peach, coconut.

Complex Fruits.—In contrast to simple fruits, there are several kinds of a complex nature, known as *aggregate, accessory,* and *multiple.*

Aggregate fruits are produced by a single flower that has a gynecium composed of several carpels close together (blackberry, raspberry).

Accessory fruits are those in which the main portion is formed from some part other than the pistil. Thus, in the strawberry the edible portion is the receptacle, while the ripened ovaries form achenes. Following Asa Gray, the strawberry may be conceived as a rose hip turned inside out.

Multiple fruits are composed of the fruits of several flowers of an inflorescence inserted close together, as in the mulberry (Fig. 397). If, as Gray also suggested, we, in imagination, turn the mulberry outside in we have the explanation of such a fruit as the fig (*synconium*) (Fig. 399).

Classification of Fruits.—For convenience of reference we give on page 409 a tabular view of the classification of fruits.

TABLE VIII.—CLASSIFICATION OF FRUITS

- **Dry Fruits**
  - **Indehiscent**
    - Nut (glans)
      - *Acorn, walnut, pecan*
    - Achene
      - *Buttercup, rose*
    - Caryopsis (Grain)
      - *Corn, cereal grains,* and *all other Grasses (Gramineae)*
    - Samara (Key)
      - *Maple, ash, elm*
  - **Dehiscent**
    - Follicle
      - *Peony, Magnolia*
    - Legume (Pod)
      - *Pea, bean, locust*
    - Loment
      - *Some clovers*
    - Silique
      - *Mustard, cabbage*
    - Capsule
      - *Poppy, Iris*
- **Succulent Fruits**
  - Drupe
    - *Cherry, walnut, coconut*
  - Berry
    - *Tomato, banana, grape*
  - Hesperidum
    - *Lemon, grape-fruit*
  - Pepo (Gourd)
    - *Cucumber, muskmelon*
  - Pome
    - *Apple, quince*

Aggregate—*Raspberry, blackberry*

Accessory—*Strawberry, rose-hip*

Multiple—*Mulberry, fig, pineapple*

CHAPTER XIX

INTERPRETATION OF THE FLOWER AND SEED

It is one thing to know the structure of flowers, but a quite different thing to be able to interpret that structure in the light of its origin. For there were not always flowers on the earth; they have gradually developed, through the untold thousands of years of the geological ages, from much more primitive structures; this is known as *floral evolution*. Now the entire story of the evolution of flowers and of flowering plants cannot be told from observation, for many of the "connecting links" have been lost; but the present-day flora contains many primitively organized descendants of the ancestors of flowering plants and, from a study of these, the main lines of the story can be told with assurance of reasonable accuracy. It seems difficult for us to imagine a time when there were no flowering plants—when the landscape, though green with the verdure of herbs, shrubs, and trees, did not contain a single plant that bore flowers, as they are now understood. Such, however, was the case, and one of the most fascinating problems of botany, for one who studies plants from the standpoint of "pure science"—that is, from the mere desire and delight of finding out and knowing how—is to unravel the story of the evolution of floral structures, and of the plants that bear them. It is not possible to understand flowers and seeds except in the light of the life-history of ferns and the plants that stand directly above them in the evolutionary scale. The salient features of this story must, therefore, be passed somewhat rapidly in review.

LIFE HISTORY OF A FERN

The Spore-bearing Phase.—The fern plant, as commonly known, comprises a crown of dark green leaves or *fronds*, borne on an underground stem or *rhizome*. The rhizome bears fibrous roots (Fig. 284). If we examine the leaves of a mature plant,

we shall find the under side of some of them thickly covered with "fruit dots," the *sori* (singular, *sorus*), commonly arranged just over a leaf-vein (Fig. 285). An examination of a sorus with the hand-lens or microscope discloses the fact that it comprises a cluster of stalked capsules or spore-cases (*sporangia*), each having a prominent row of cells, the *annulus*, and containing an even

FIG. 284.—Cluster of plants of Christmas fern (*Polystichum acrostichoides*). (Photo by Elsie M. Kittredge.)

number of tiny brown bodies, the *spores* (Fig. 286). The cluster of sporangia is covered with a delicate membrane, the *indusium;* this may be absent in some species of fern. In the common brake (*Pteridium aquilinum*) the spore-cases are borne along the margins of the frond, and the indusium is a continuous delicate flap of marginal tissue that folds over so as to cover and protect the spore-cases (Fig. 287). Leaves that bear spores are *sporophylls.*

The spore-case always contains an even number of spores, commonly 64. It is easy to calculate, approximately, the enormous number of spores borne by a mature plant having, say, ten sporophylls. There may be as many as 1000 sori on each sporophyll, and each sorus may contain 100 sporangia.

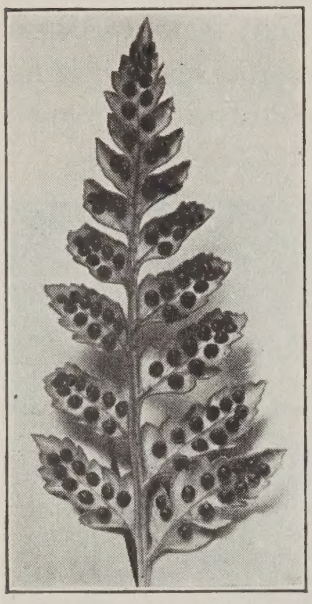


FIG. 285.—Portion of a sporophyll of the fern, *Polystichum adiantiforme*, showing the "fruit-dots" or sori on the under surface.

$$64 \times 100 \times 1000 \times 10 = 64{,}000{,}000$$

Thus over sixty million spores may be the product of one plant. Since the fern plant bears spores it is termed a *sporophyte* (spore-bearing plant). It should be noted that the *spores result merely* from *cell-division*, a purely vegetative process.

The Sexual Phase.—When the spores are mature the annulus bends back, rupturing the spore-case, and then very suddenly springs again into its initial position, with sufficient force to throw the spores out to some distance. They fall to the ground and under suitable conditions of temperature, moisture, and light, they begin to *germinate*, sending out a tiny green filament, the *protonema* (first thread). By successive cell-divisions the protonema develops into a flat, more or less heart-

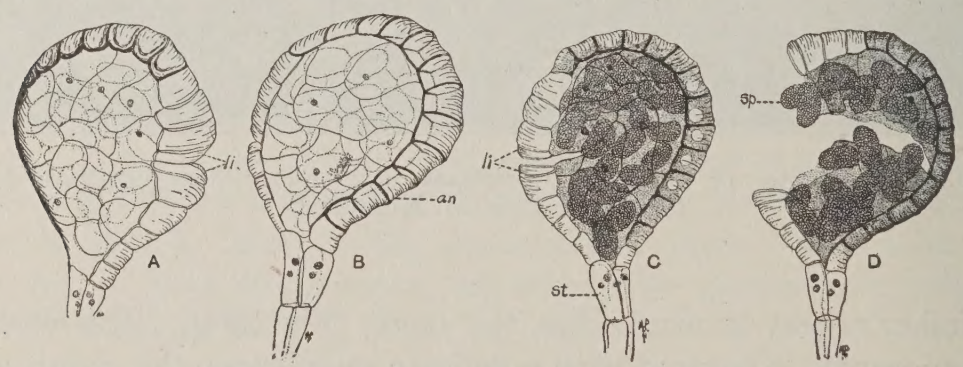


FIG. 286.—Sporangia of an undetermined species of fern; *li*, lip-cells; *an*, annulus; *st*, stalk; *sp*, mature spores. Each of the four nuclei in the upper cells of the stalk is in the terminal cell of one of the four rows of cells that compose the stalk.

shaped, green body, the *prothallus* (*prothallium*) (Figs. 288–290). The underside of the prothallus develops a large number

of colorless, thread-like bodies, called *rhizoids* because they act like roots in holding the prothallus fast to the soil (or other substratum), and take in water and dissolved substances from the soil. At and near the edges the prothallus is commonly only one cell thick, but the part near the notch is several cells in thickness, and is called the *cushion* (Fig. 290).

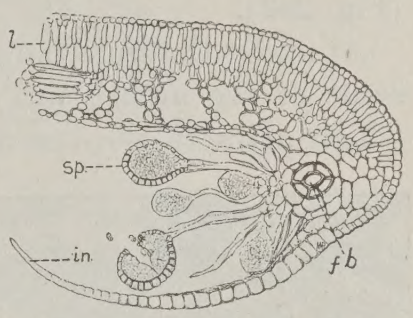


FIG. 287.—Cross-section through the marginal sorus of a sporophyll of the bracken fern (*Pteridium aquilinum*). *l*, palisade layer; *fb*, vascular bundle; *sp*, sporangium; *in*, indusium. (Greatly magnified.)

On the underside of the cushion there develop several tiny flask-shaped bodies, the *archegonia*. Each archegonium consists of a basal portion (the *venter*), and the *neck*. The venter, when mature, contains a single large cell, rich in protoplasm, and called the *egg-cell*, or *egg*. A *neck-canal* extends down through the neck to the cavity of the venter. This canal results from the disintegration of a row of *neck-canal-cells* (Fig. 291).

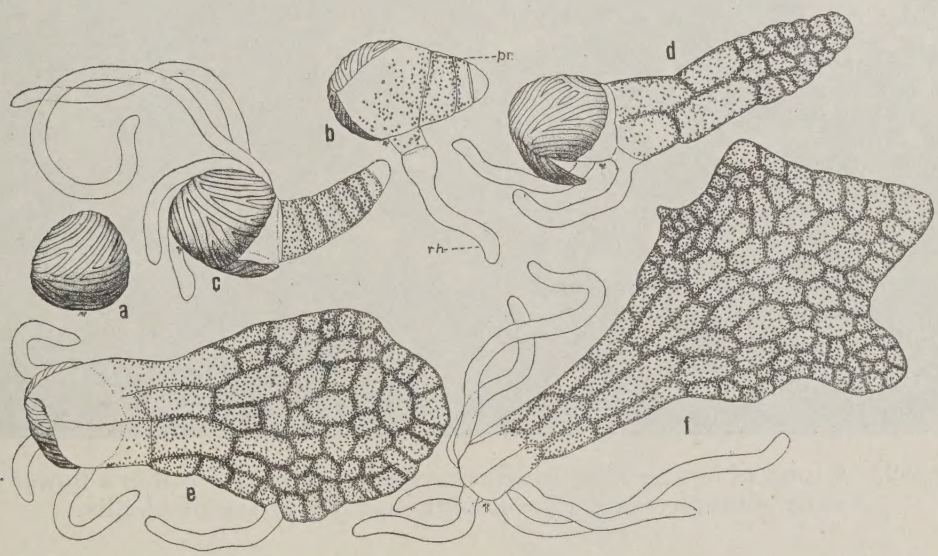


FIG. 288.—Germination of the spores of a fern. *a*, Before germination; *b*, early stage, showing protonema (*pr.*), and first rhizoid (rh); *c*, *d*, *e*, *f*, successive stages in the development of the prothallus.

Among the rhizoids, between the cushion and the apex, occur many other small bodies, the *antheridia*, much simpler in structure, and much more numerous than the archegonia. When mature the antheridia contain numerous tiny sperm-cells or

sperms. Each sperm consists of a single cell bearing numerous delicate lashes or *cilia.* By the vigorous motion of the cilia the sperms swim about in water; a thin film of water is sufficient (Fig. 292).

At about the time the sperms are escaping from the antheridia some of the archegonia are secreting a substance (malic acid) which attracts the sperms; they swim toward the archegonia,

FIG. 289.—Group of fern prothallia growing on the surface of soil in a flower pot. Young sporophytes are developing on some of the prothallia.

and down the neck-canal to the egg in the venter. The head of the sperm enters the egg, and eventually the nucleus of the sperm-cell unites with the nucleus of the egg-cell, thus completing the act known as fertilization (Fig. 293).

Egg-cells and sperm-cells are often referred to by the common or generic name, *gametes;* and, since the prothallus bears the gametes it is called a gamete-bearing plant, or *gametophyte.*

The Nature of the Fertilized Egg.—We noted above that the spores are the result merely of cell-division; in contrast, we see

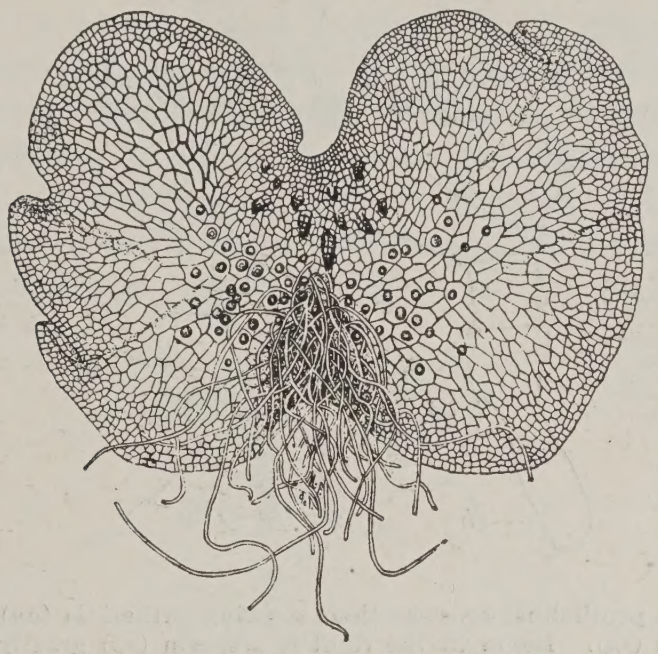


FIG. 290.—Prothallus of a fern. Archegonia on the (central) cushion, near the notch; antheridia among the rhizoids, below. (After Margaret C. Ferguson.)

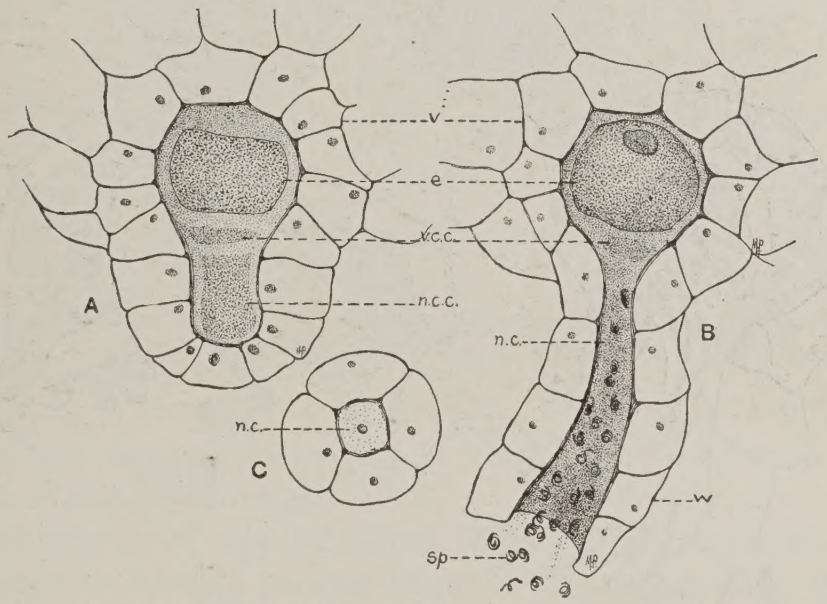


FIG. 291.—Archegonia of a fern (*Adiantum*). *A*, young archegonium; *B*, mature; *C*, top view, showing terminal cells of the four rows of wall cells; *v*, wall of venter; *e*, egg; *v.c.c.*, ventral canal-cell; *n.c.*, neck-canal; *sp*, sperms entering the neck-canal. *A* and *B* in longitudinal section.

that *the fertilized egg is the result of cell-fusion.* This is the essential fact in sexual reproduction, as compared with asexual repro-

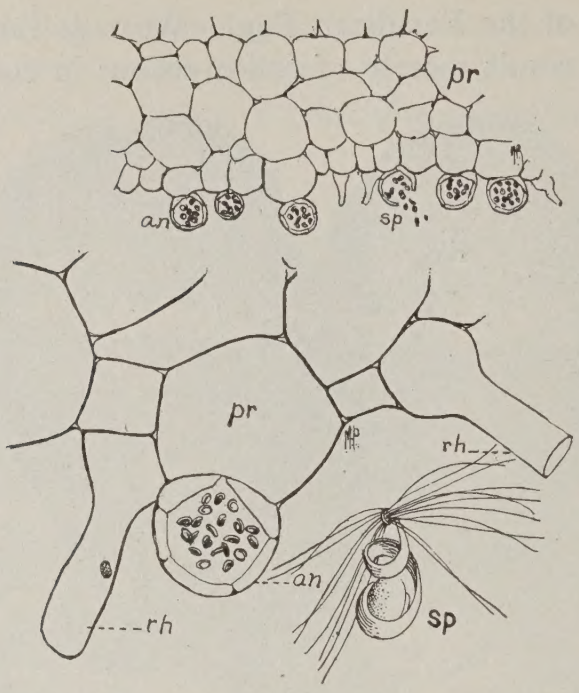


FIG. 292.—Fern prothallus; cross-sections showing antheridia (*an*), sperms (*sp*), and rhizoids (*rh*). Below at the right is a sperm (*sp*) greatly enlarged.

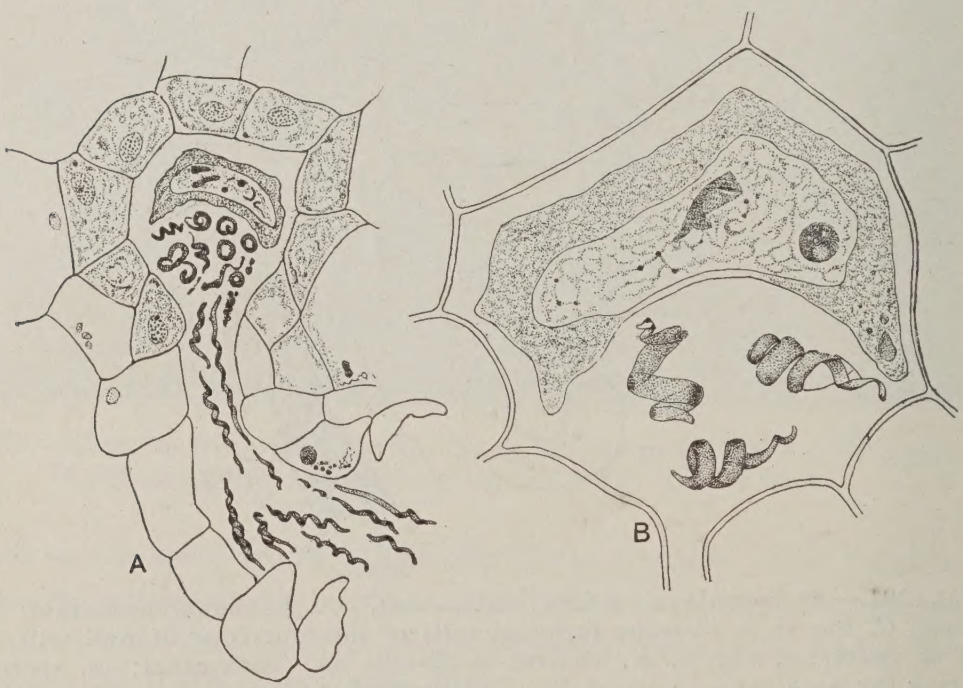


FIG. 293.—Fertilization in the fern, *Onoclea*. *A*, longitudinal section of archegonium, showing the egg in the venter, and numerous sperms passing down the neck-canal. *B*, an egg-cell in the venter. One sperm has entered the nucleus, three sperms have failed to enter the egg. (After W. R. Shaw.)

duction and vegetative propagation. The fertilized egg is variously referred to as an *oösperm* (egg and sperm), or *oöspore* (egg-spore); it is also called a *zygote* (Greek, ζυγωτός—*zygotos*, yoking), indicating its formation by the yoking together or fusion of the male and female gametes. It will be recognized at once that, by virtue of its origin, the oösperm is of double or *diploid* nature, comprising material from two parents. This is in contrast to the spore, which is simple or *haploid*, being derived (asexually) from only one parent. The simplification resulting by

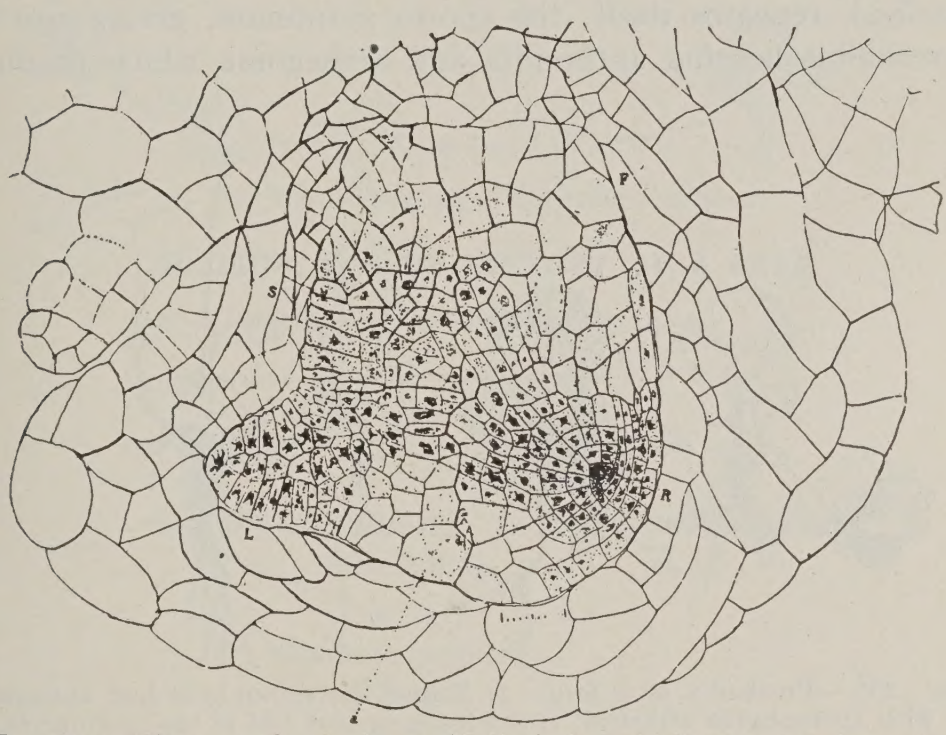


FIG. 294.—Young embryo of a maidenhair fern (*Adiantum concinnum*); still surrounded by the archegonium, which has grown in size. *L*, leaf; *S*, stem; *R*, root; *F*, foot. (After Atkinson.)

cell-division in spore-formation is restored by cell-fusion in the formation of the gametes.

Development of the Fertilized Egg.—After fertilization the egg begins to divide, passing from its one-celled stage through two, four, eight, et cetera, to a many-celled stage. This many-celled structure is called the *embryo* (Fig. 294). Early in its development the embryo becomes differentiated into four well marked regions from which there develop, respectively, a root, stem, leaves, and a fourth organ called the *foot*. The foot serves to absorb nourishment for the young embryo from the

prothallus. The development of the embryo is continuous; that is, *no resting period intervenes* before the resulting plant becomes independently established, with its rhizome and roots in the soil, and its green leaves expanded in the air and sunlight (Fig. 295). The prothallus, in the meantime, exhausted by nourishing the embryo, has died.

Alternation of Generations.—Sori eventually develop on the under side of the leaves, their sporangia mature and scatter spores and the life-cycle of processes and structures, above described, repeates itself; the spores germinate, giving rise to a prothallus bearing antheridia and archegonia which produce

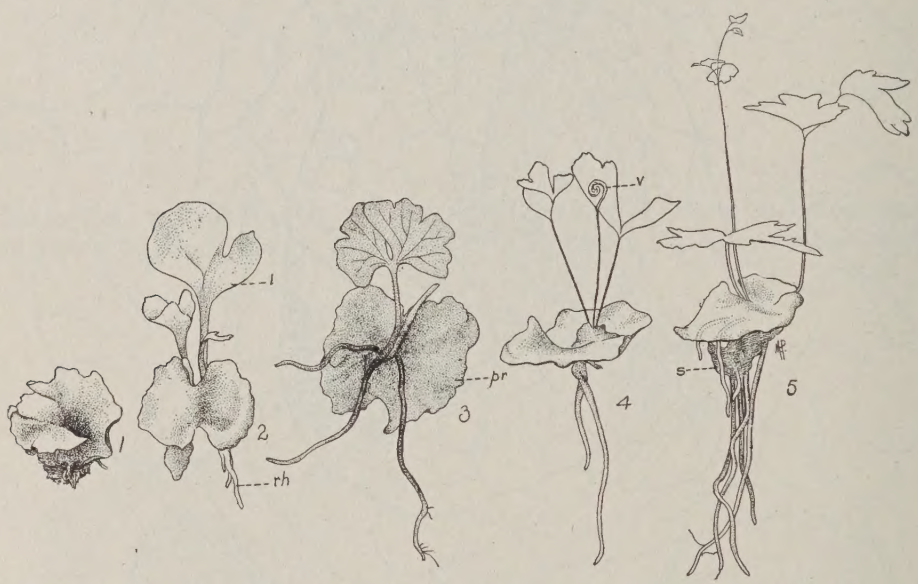


FIG. 295.—Prothallia of a fern. 1, Before the sporophyte had appeared; 2–5, with sporophytes attached; *l*, cotyledon or first leaf of the sporophyte; *v*, circinate vernation of a leaf; *s*, mass of soil adhering to the rhizoids and roots.

eggs and sperms. After fertilization the eggs (zygotes) develop into embryos which, *without any period of rest*, grow into mature sporophytes, bearing spores. Cell-fusions alternate with cell-divisions, zygotes with spores, sexual reproduction with asexual, gametophyte with sporophyte. The alternation of the gametophyte generation with the sporophyte generation is known as *alternation of generations*. This phenomenon is not confined to ferns but is one of the most fundamental facts in the life-history of nearly all plants.

The life-history of the fern is stated in tabular form on page 419, and is shown diagramatically in figure 296.

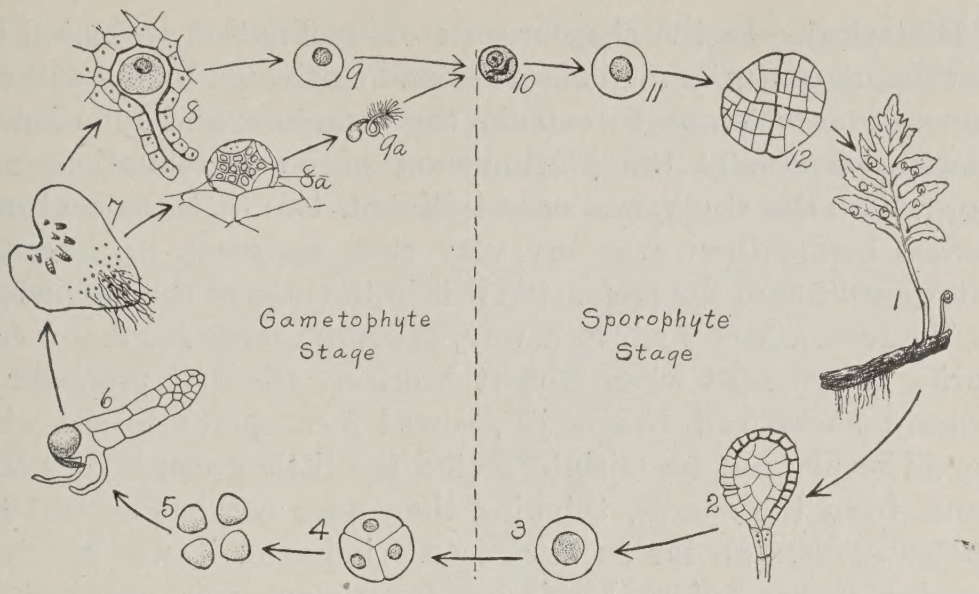


FIG. 296.—Diagram of life-cycle of a fern.

OUTLINE OF LIFE HISTORY OF A FERN

Gametophyte (prothallus)

Antheridium — Archegonium

Sperm (male gamete) — Egg (female gamete)

Fertilization

Oösperm (zygote)

Embryo

Mature sporophyte (mature zygote)

Sporophyll

Sporangium

Spore-mother-cell

Reduction

Spore Spore Spore Spore

Gametophyte

Historical.—In the chapter on cross-pollination we noted for how many centuries men observed and cultivated plants without any serious attempt to explain the structure and function of flowers—especially the phenomenon of cross-pollination, and how, after the study was once initiated, two or three centuries passed before there was any very close approach to a correct interpretation of the facts. So it is in the case of the life history of the fern. Men had, in a way, observed ferns for many centuries before 1683 when Robert Morison, the first professor of botany at Oxford University, sowed fern spores to see what would result; but he misinterpreted the little green bodies that came from the spores, thinking they were cotyledons and the spores seeds. So far as our records indicate, it was nearly a hundred years before Morison's experiment was repeated by John Lindsay.[1] Further advance in our knowledge awaited the improvement of the compound miscroscope in the first quarter of the nineteenth century. Following this, Hofmeister (1841) and Suminski (1848) worked out and described the broad outlines of the life history substantially as we know it today.

LIFE HISTORY OF A LITTLE-CLUB-MOSS (*Selaginella*)

In the life history of the fern we have found little to suggest, at first thought, either a flower or a seed. A study of the fern, however, enables us to understand the life history of the more highly organized little-club-moss, *Selaginella*. There are over three hundred species of *Selaginella*, widely distributed over the world; as an example we choose *Selaginella Martensii*, a tropical form common in conservatories in the north.

The Spore-bearing Plant.—The sporophyte consists of a much-branched stem, bearing scale-like, but green, foliage leaves, sessile and more or less closely appressed to the stem. Near the tips of the branches the foliage leaves give place to sporophylls, also green, and so arranged as to form a distinct *cone* (Figs. 297 and 298).

If we examine a longitudinal section of a cone, we shall normally find a sporangium, not borne on the blade of the sporophyll,

[1] A practical result of Lindsay's experiments was the discovery that tropical ferns could be transported from the West Indies to Europe merely by sending the spores, from which new plants could be raised in the greenhouse.

as in the fern, but in its axil. Occasionally the lower leaves of the cone are sterile, *i.e.*, they have no sporangia in their axils. Closer examination discloses the fact that there are two kinds or sizes of spores—large spores (*megaspores*), and small spores (*microspores*). Corresponding to these terms we have *megasporangia* on *megas-*

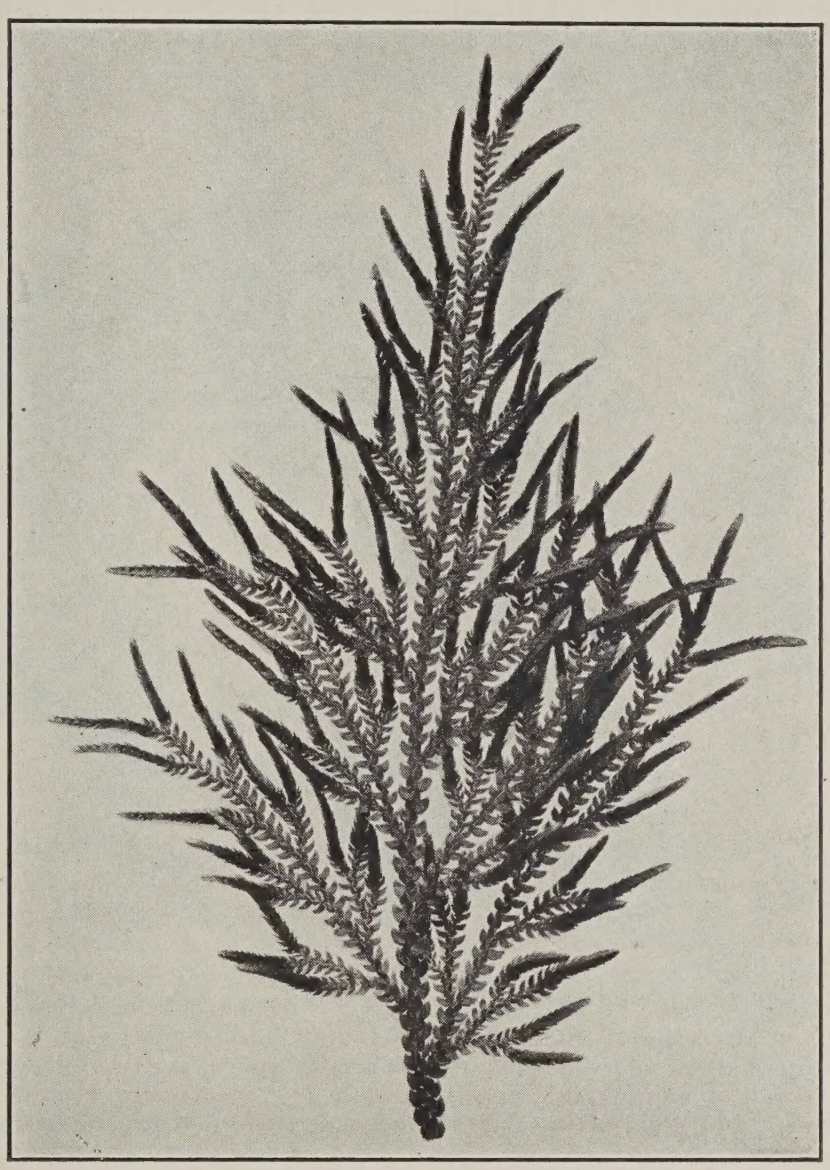


FIG. 297.—*Selaginella amoena*. Branch bearing numerous terminal cones.

porophylls and *microsporangia* on *microsporophylls*. Sometimes the megasporophylls are confined to the lower portion of the cone with the microsporophylls occupying the upper portion, or, in other species, the megasporophylls and microsporophylls alternate with each other along the axis of the cone (Fig. 298). The

habit of bearing spores of two sizes is called *heterospory* (spores unlike), and the plant is called *heterosporous*. In contrast, a plant like the fern, having spores of only one size, is called *homosporous* (spores alike) and the habit *homospory*.

The Gametophytes.—The germination of the microspore is largely confined to cell-divisions, and *the male gametophyte is*

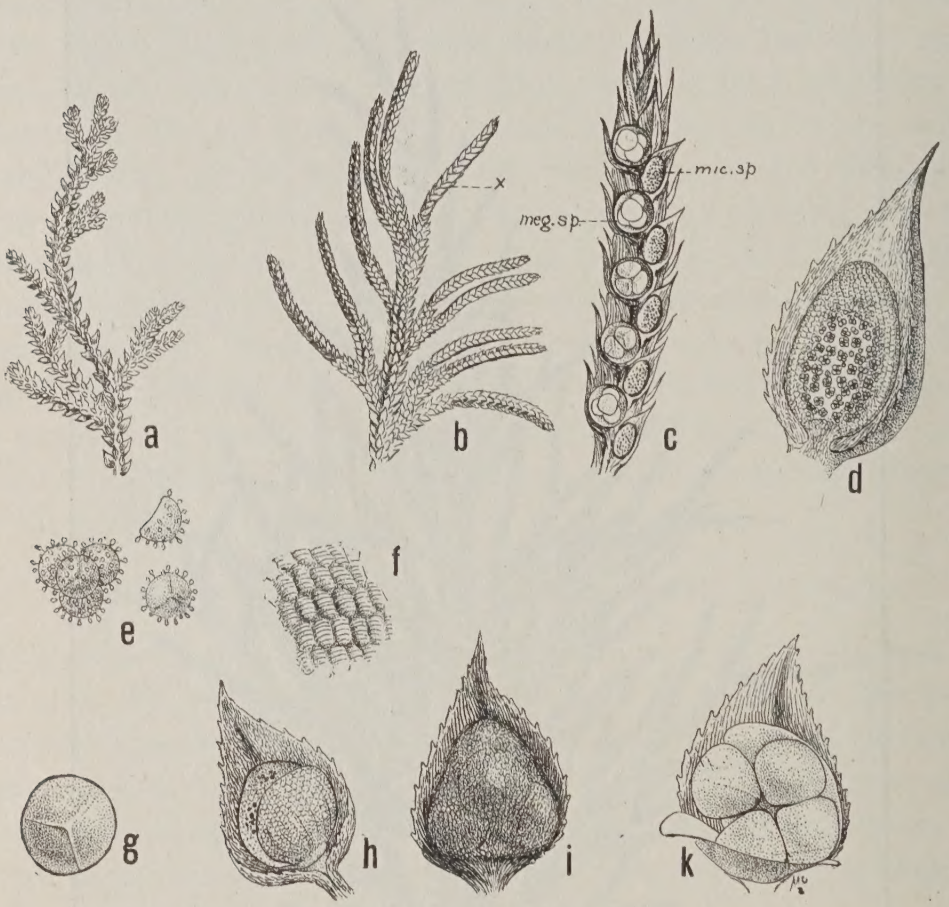


FIG. 298.—*Selaginella Martensii*. *a*, vegetative branch; *b*, portion of the stem, bearing cones (x); *c*, longitudinal section of a cone, showing microsporangia (*mic. sp.*) in the axils of microsporophylls, and megasporangia in the axils of megasporophylls; *d*, microsporangium with microsporophyll; *e*, microspores; *f*, portion of wall of sporangium, greatly magnified; *g*, megaspore; *h*, microsporangium opened, and most of the microspores scattered; *i*, megasporangium, with megasporophyll; *k*, same, opened, showing the four megaspores.

developed entirely within the wall of the microspore. It is a much simpler structure than the prothallus of the fern, comprising only one vegetative cell and one antheridium containing four sperms.

The megaspores begin to germinate while still in the sporangium. Germination consists of a series of cell-divisions and growth, resulting in a globular female gametophyte, bearing several

archegonia. As the female gametophyte enlarges it bursts open the walls of the megaspore, and the part bearing the archegonia protrudes (Figs. 298, and 299).

It should be noted that the female gametophyte does not develop chlorophyll, but lives throughout life as a parasite on the parental sporophyte, from which is derived all the food for the nourishment of the embryo. Fertilization takes place somewhat as in the ferns, the sperms swimming to and into the

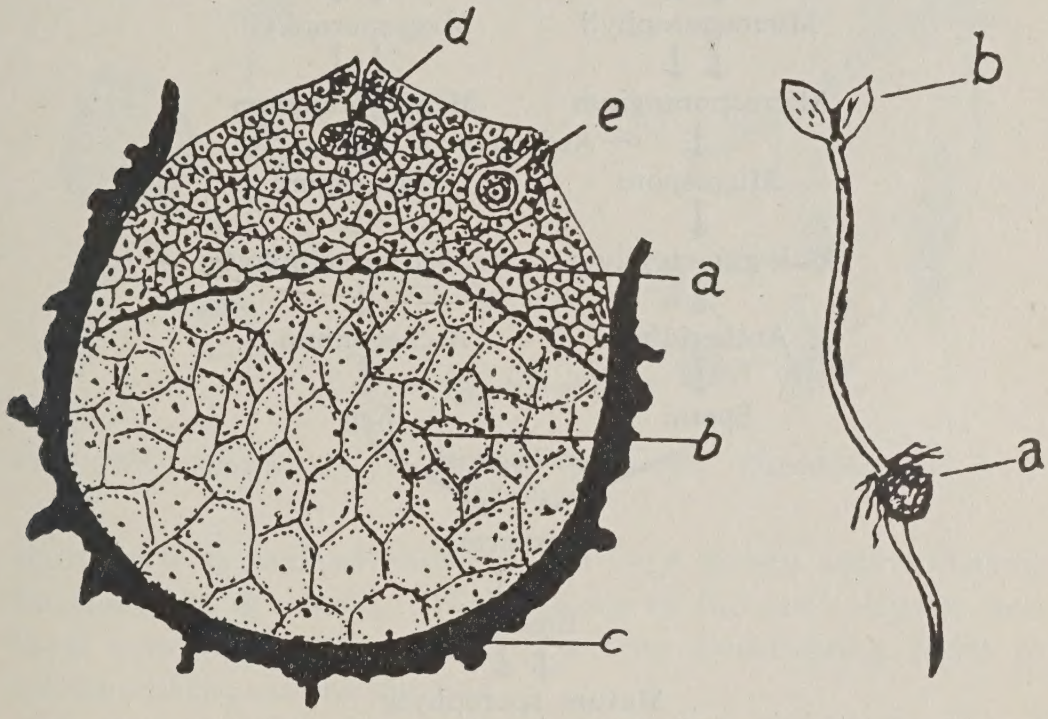


FIG. 299.—*Selaginella*. At the left, a germinating megaspore in longitudinal section, × about 100. *a*, reproductive and *b*, vegetative part of the female gametophyte; *c*, spore-coat; *d*, embryo, and *e*, an egg-cell, each in the venter of an archegonium. At the right, a young sporophyte developed from an embryo in an archegonium of the gametophyte, which is partly enclosed by the spore-coat of the megaspore, *a*. (From Dixon. The left hand figure after Lyon.)

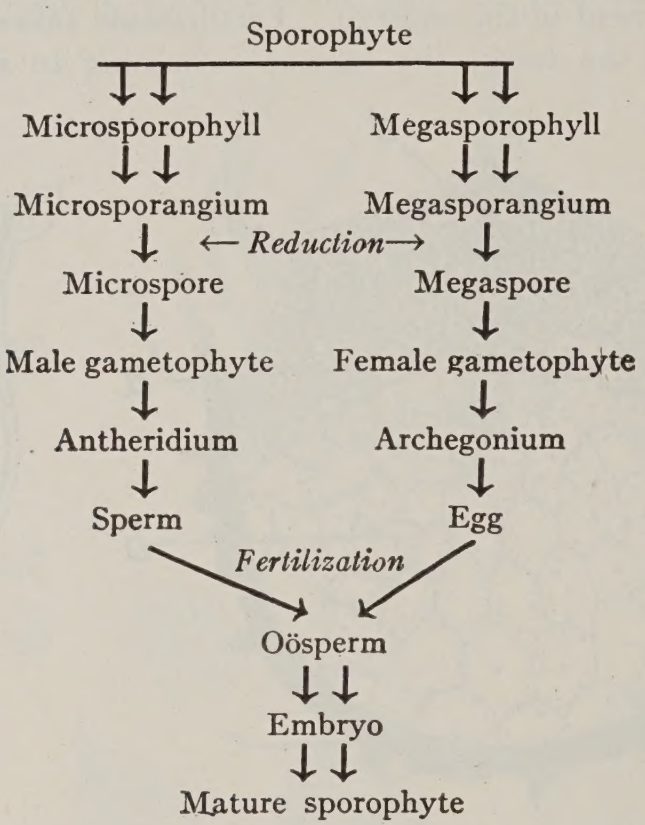
archegonia, where they fuse with the eggs. The fertilized egg begins at once to develop, and the embryo has no resting period but continues uninterrupted growth until its root and shoot, with two cotyledons, emerge from the prothallus, and the young sporophyte gradually becomes established as an independent green plant. This life history is shown in tabular form on page 424, and diagramatically in figure 299*a*.

A "Near-seed."—In ferns and other plants below *Selaginella* in the scale of life, structural differentiations associated with sex are confined to the gametophyte, but in *Selaginella* they are found

also in the sporophyte, with its micro- and megasporophylls and micro- and megasporagnia. There are also three other facts of outstanding importance with reference to the evolution of seeds:

1. The entire dependence of the gametophyte on the sporophyte for nutrition.

OUTLINE OF LIFE HISTORY OF SELAGINELLA



2. The reduction of the vegetative tissue of the gametophytes (to only two or three cells in the case of the male gametophyte).

3. The retention of the female gametophyte, throughout its entire existence, entirely within the wall of the megaspore.

It will be seen at once that *if* the embryo of *Selaginella* should enter upon a period of rest before developing into a mature sporophyte, and *if* the female gametophyte remained *entirely* within the wall of the megaspore, we should have a very close approximation to such a seed as that of the pine tree or of Indian corn—a structure that could be kept over winter and planted in the spring. Two species of *Selaginella* (*S. rupestris* and *S. apus*) have been reported by Miss Lyon[1] as forming embryos (in autumn)

[1] Lyon, Florence. Another seed-like characteristic of Selaginella. Bot. Gaz. **40**: 73. July, 1905.

which may resume growth after a period of rest. In fact, *S. rupestris* undergoes a reduction in the number of megaspores, such as occurs in the seed-bearing plants, and retains its megaspores "throughout their germination, and even until the young

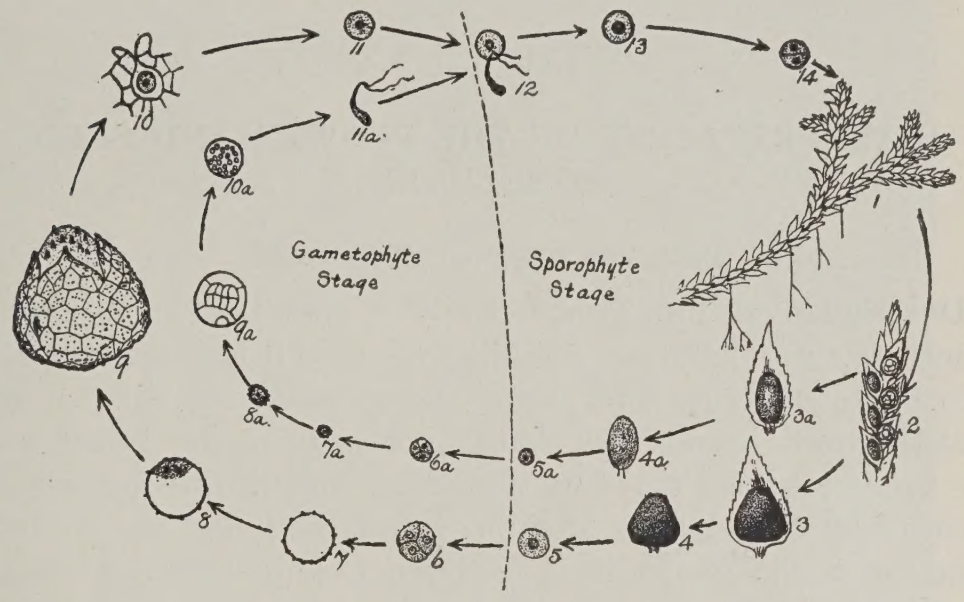


FIG. 299*a*.—Diagram of life-cycle of *Selaginella*. (Modified from J. H. Schaffner.)

sporophyte is well advanced," thus very closely approximating the behavior of a seed. We shall see in the next chapter how these conditions are realized in a true seed-bearing plant or *spermatophyte*, such as the pine.

CHAPTER XX

INTERPRETATION OF THE FLOWER AND SEED (CONCLUDED)

LIFE HISTORY OF THE PINE

Description of the Tree.—While a pine tree is a familiar object, few who have not carefully observed it have a very exact idea of its structure and parts. Everyone knows, for example, that the trunk is *excurrent*, that is, it may be clearly traced from the ground to the tip of the tree (Fig. 300); it does not lose its identity by branching or dividing into large limbs, *i.e.*, it is not *deliquescent*, like the trunk of an elm or an apple tree. An excurrent trunk results from the persistence, year after year, of a terminal bud which determines the growth of the trunk as a single shaft, often reaching a height of 160 feet.

The branches appear to be arranged in *whorls*, but close observation discloses the fact that they are only pseudo-whorls, for the branches do not all arise at precisely the same level on the trunk, as in true whorls. The lower branches are longer than those above because they have had a longer period of growth, and also because they have grown in more shade than the upper branches, and light tends to retard the rate of growth in length of stems and branches of the pine. This arrangement of length of branches gives the tree as a whole its cone-like shape, especially when it grows free in the open. When trees grow together in a forest the mutual crowding and shading result in *natural pruning*, by which the lower branches are eliminated early in the life of the tree (Fig. 300). Lumber sawed from such trunks is relatively or quite free from *knots*, for knots in lumber are only cross-sections of lateral branches which have remained on the tree while the trunk was increasing in thickness. Under such circumstances the new wood each year is laid down around the branch; if the branch continues its own growth a "live knot" results, if the branch dies

we have a "dead knot," which is easily pushed out of the board, leaving a "knot hole."

FIG. 300.—Grove of pine trees showing excurrent trunks and also natural pruning.

There are five fairly distinct kinds of leaves on a pine tree, as follows:

1. *Foliage leaves,* known as "pine needles." In young trees and saplings these occur on the trunk as well as on the branches, but in older trees they are chiefly or wholly confined to the branches. They occur singly or in bundles or fascicles of two,

three, or five, the number being characteristic for each species, *e.g. two* in the Canadian or Red Pine (*P. resinosa*) and the Jersey or Scrub Pine (*P. Virginiana*); *three* in Georgia Pine (*P. palustris*), Western Yellow Pine (*P. ponderosa*), and Pitch Pine (*P. rigida*); and *five* in the White Pine (*P. Strobus*). Since the leaves remain on for from two to ten years, the tree as a whole is "evergreen."

FIG. 301.—Scotch pine (*Pinus sylvestris*). Branch bearing carpellate cones, one month, and two and three years old. (Cf. Fig. 302.)

REPRODUCTION

Seed-bearing Cones.—Everyone knows that pine seeds are borne in the cones. The new cones appear *near* the tip of the new growth in early spring, more or less conspicuous for their reddish color (Figs. 301 and 302). The cone is really a modified branch.

On the ventral surface of each cone-scale are two tiny, naked ovules (Fig. 302). Since they are naked (*i.e.*, not inclosed in an ovary) the tree is called a "naked-seeded" tree, or *gymnosperm.* The ovule-bearing scale functions as a carpel, and the cone is called a *carpellate cone.*

Each ovule comprises an outer covering or *integument*, surrounding an inner structure, the *nucellus* (Fig. 303). At the apex

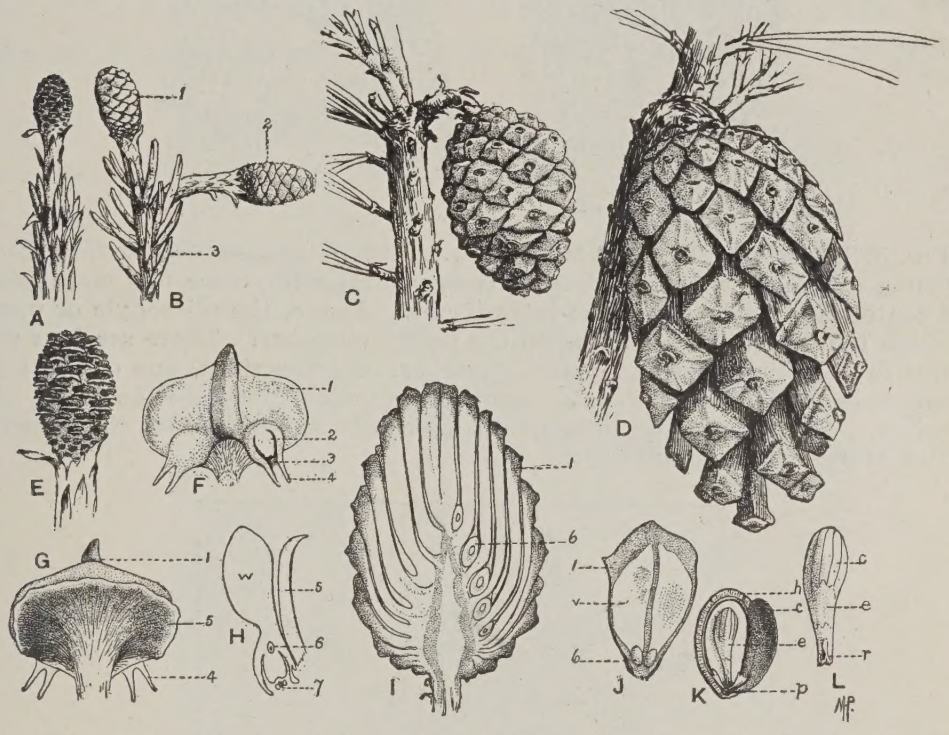


FIG. 302.—Scotch pine (*Pinus sylvestris*). *A-D*, stages in the development of the carpellate cone, and its carpotropic movements. *E*, very young carpellate cone much enlarged; *F*, ventral, *G*, dorsal views of a scale from *E*; 1, ovuliferous scale; 2, ovule (in longitudinal section); 3, pollen chamber and micropyle leading to the apex of the nucellus (megasporangium); 4, integument of the ovule; *G*, 1, tip of ovuliferous scale; 5, bract; 4, integument; *H*, longitudinal section, at right angles to the surface, of the ovuliferous scale (diagrammatic); 6, female gametophyte; *I*, longitudinal section of a mature cone, 6, seed; *J*, scale from a mature cone; 6, seed; *W*, wing of seed; *K*, dissection of mature seed; *h*, hard seed coat; *c*, dry membraneous remains of the nucellus, here folded back to show the endosperm and embryo; *e*, embryo; *p*, remains of nucellus; *L*, embryo; *c*, cotyledons; *e*, hypocotyl; *r*, root-end.

of the nucellus the integument does not quite come together, thus leaving a tiny passage or channel, the *micropyle* (little gateway), which leads to the *pollen-chamber.* Within the young nucellus there may be found, at the proper season, three or four *megaspores.* Normally, only one megaspore germinates, the others disorganizing and furnishing nourishment for the one that germinates.

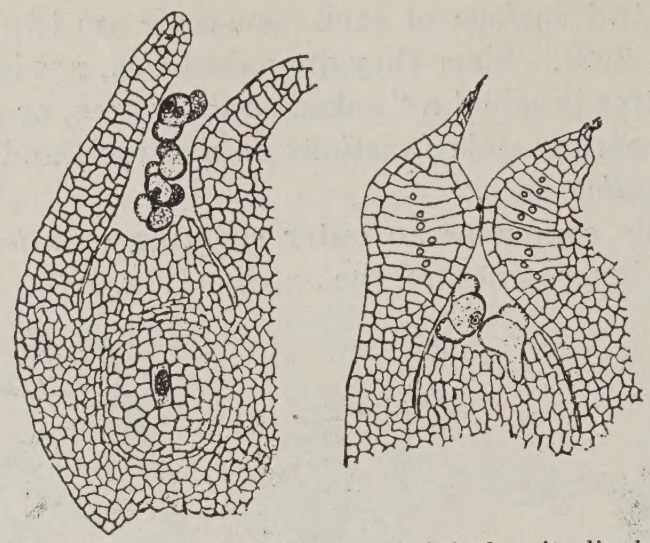


FIG. 303.—White Pine (*Pinus Strobus*). At left, longitudinal section through a young ovule showing the nucellus (megasporangium) with one megaspore in the center, and enclosed by the integument. Above, the micropyle or opening through the integument, leading to the pollen chamber. There are four pollen grains in the micropyle and pollen chamber. At the right, one of the pollen-grains is beginning to germinate, sending the pollen-tube into the tissue of the nucellus. The cells of the integument have enlarged and closed the micropyle. (After Margaret C. Ferguson.)

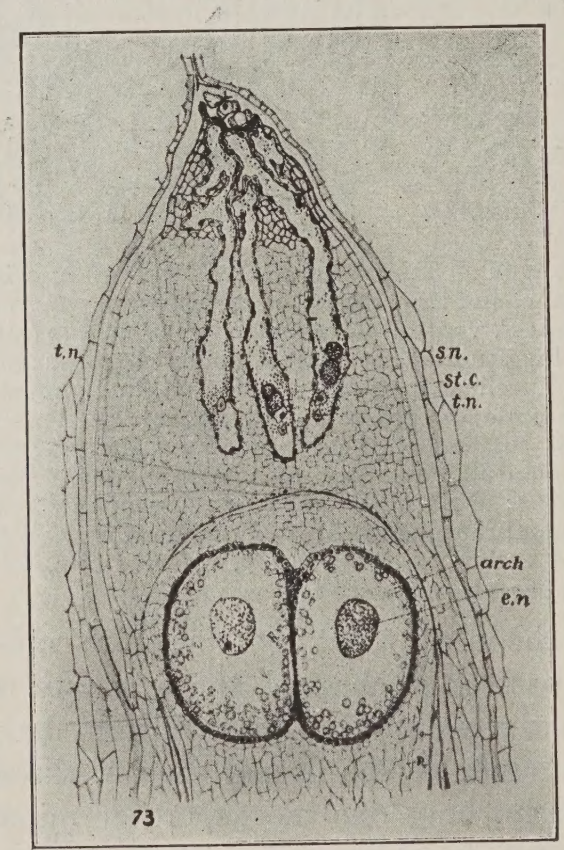


FIG. 304.—White pine (*Pinus Strobus*). Vertical section through the upper part of an ovule, shortly before fertilization. *s.n.*, sperm-nuclei; *st.c.*, stalk-cell; *t.n.*, tube-nucleus; *arch*, archegonium; *e.n.*, egg-nucleus. (After Margaret C. Ferguson.)

As in the case of the little-club-moss, the megaspore develops into a *female gametophyte.* This gametophyte passes its entire life as a parasite, living on the tissue of the nucellus; it is a simple mass of cells, undifferentiated except for the formation of two to five somewhat reduced *archegonia* at the micropylar end. Within the venter of each archegonium is an egg (Fig. 304).

Staminate Cones.—Staminate, or pollen-bearing, cones occur on the same tree that bears the carpellate cones. The pine is, therefore, monoecious. The staminate cones appear in spring—

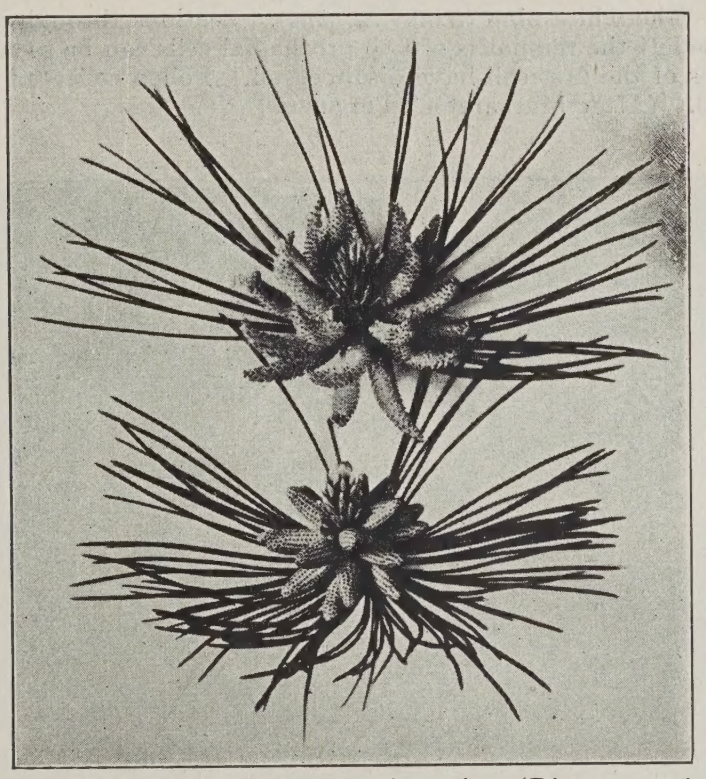


FIG. 305.—Staminate cones of the Austrian pine (*Pinus austriaca*). Below, before shedding pollen; above, after shedding.

usually in May in the Northern States—and persist for a few weeks only. They occur as lateral branches on the current year's growth (Fig. 305). On the underside of the young scales are the spore-cases or *sporangia,* bearing *microspores.* The main body of each microspore bears two tiny air-sacs which add greatly to the buoyancy of the spores in the air.

The germination of the microspore consists only of cell-divisions, giving rise to a very simply organized *male gametophyte,* consisting of only two *vegetative cells,* one *mother-cell of an antheridium,* and

a *tube-cell.* Only remnants of the prothallial cells can be seen in the mature gametophyte. At this stage the structure is known as a pollen-grain (Fig. 306).

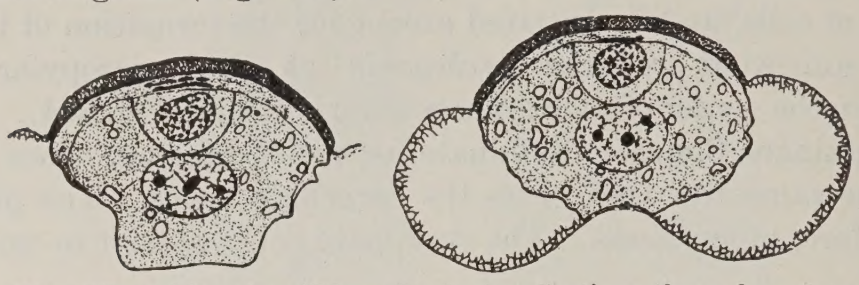


FIG. 306.—The white pine (*Pinus Strobus*). Sections through mature pollen grains; at the left the remnants of two prothallial cells can be seen, while at the right all signs of the first cell have disappeared. Pollen collected June 9, 1898. × about 600. (After Margaret C. Ferguson.)

FIG. 307.—Shedding of pollen from a young pine tree. Note the cloud of pollen at the left, caused by shaking the tree.

Pollination occurs when the prothallus or pollen-grain is mature, usually early in June (at, *e.g.*, Ithaca, N.Y.), the exact date varying with locality, latitude, and other factors. At about the time

the pollen is being shed the axes of both the carpellate and staminate cones elongate, separating the scales; the walls of the microsporangia split, and the least jar sends the pollen out, often in perfect clouds (Fig. 307). It floats away to the carpellate cones of the same, or of different trees, and some of it finds its way up between the carpellate cones to the micropyles of the ovules, and down this passage to the pollen chamber in contact with the female gametophyte.

The pollen germinates[1] in the pollen-chamber, sending out a long *pollen-tube*,

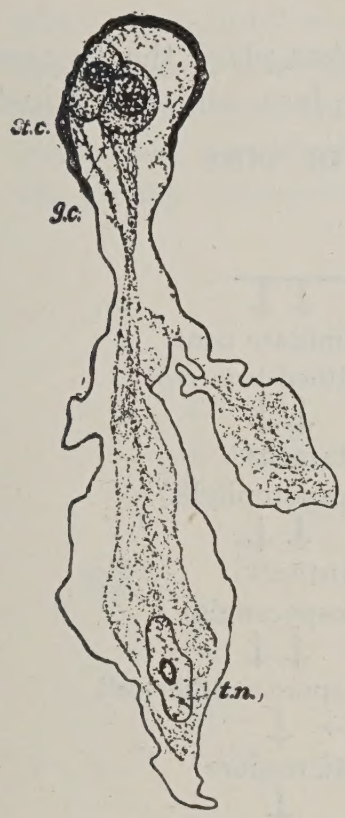


Fig. 308.

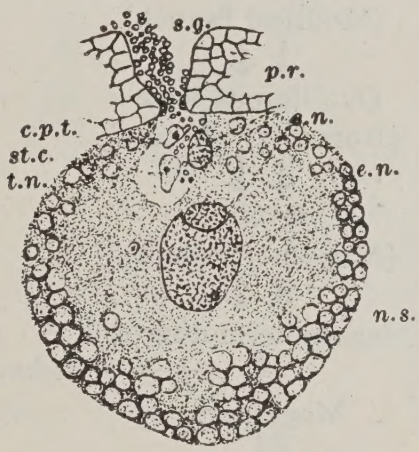


Fig. 309.

Fig. 308.—White pine (*Pinus Strobus*). Germinating pollen tube on Jan. 4, 1899. *st.c*, stalk-cell; *g.c*, generative cell; *t.n*, tube-nucleus. × about 326. (After Margaret C. Ferguson.)

Fig. 309.—White pine (*Pinus Strobus*). Longitudinal section through an archegonium at the time of fertilization. Above the fusing nuclei are various other elements emptied into the egg from the pollen-tube. Collected June 21, 1898. × about 62. *s.g*, starch grains; *p.r*, prothallium; *c.p.t*, cytoplasm from pollen-tube; *st.c*, stalk-cell; *t.n*, tube-nucleus; *s.n*, sperm-nucleus; *e.n*, egg-nucleus; *n.s*, nutritive spheres. (After Margaret C. Ferguson.)

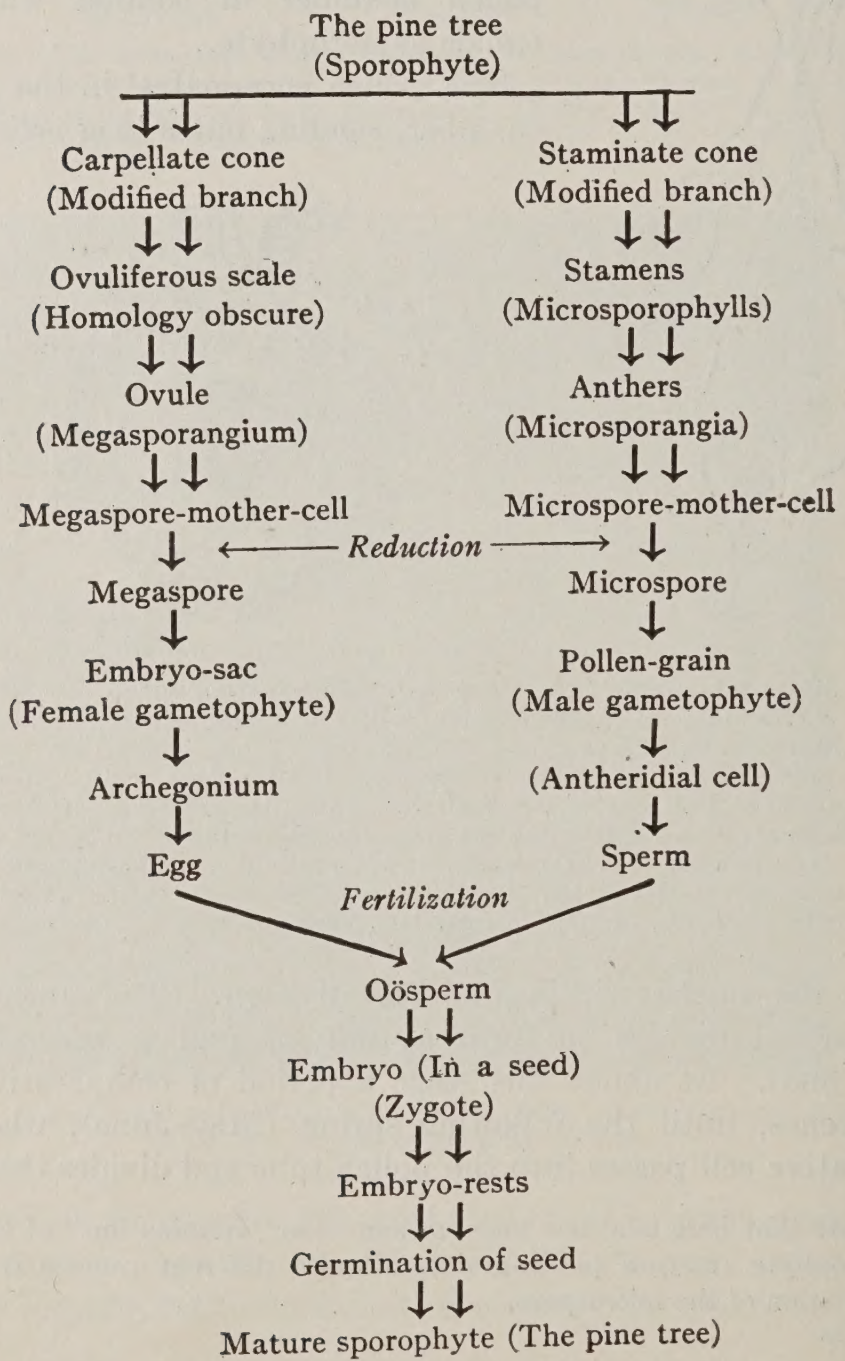
while the nuclei within undergo division. The antheridial, mother-cell divides to form a *wall-cell* and a *generative-cell* (Fig. 308). At about this stage a period of comparative rest intervenes, until the following spring (May–June), when the generative cell passes into the pollen-tube and divides there into

[1] Note that here is a new phenomenon—the "germination" of the male gametophyte (mature pollen-grain), a quite different process from the germination of the microspore.

two *sperm-cells*. The pollen-tube passes into the archegonium and discharges the two sperm-cells which find their way into the venter, and to the egg, now mature. As in the fern and little-club-moss, fertilization results from the fusion of the egg and sperm (Fig. 309).

Formation of the Seed.—There now takes place the process which was only dimly foreshadowed in the fern, and which just

OUTLINE OF LIFE HISTORY OF PINE



misses of accomplishment in *Selaginella*, namely, the formation of a true seed. The fertilized egg, by a series of cell-divisions, develops into an embryo,[1] while at the same time the tissues of the ovule become transformed. A portion of the female gametophyte (nucellus) is absorbed as nourishment by the growing embryo, but most of it becomes stored as *endosperm* around the mature embryo; the remains of the nucellus persist as a thin membrane surrounding the endosperm,[2] and the integument of the ovule becomes transformed into a hard, brown *seed-coat*.

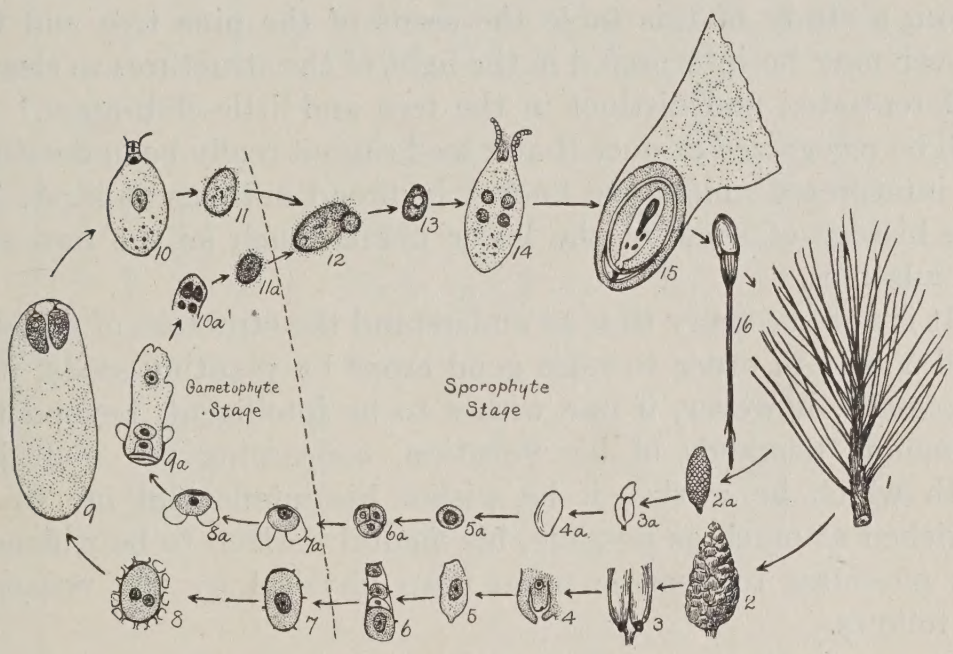


FIG. 310.—Diagram of the life-cycle of a pine. (After Schaffner.)

From the integument there also develops a thin, brown, membranous *wing*. This entire structure (the embryo, surrounded by endosperm and nucellar membrane, and the whole enclosed by the winged seed-coat) is the seed (Fig. 302, J, K, L.). We note that it takes about 18 months from pollination to make a pine seed. *The essential part of a seed is the embryo*, which in most

[1] In *Pinus* the oösperm gives rise to three distinct structures—a *proembryo*, a *suspensor*, and the *embryo*. The details need not be gone into here.

[2] As noted on page 354, in the seeds of some of the higher plants the tissue of the nucellus becomes filled with nourishment stored for the use of the developing embryo. It is then called *perisperm*.

seeds, undergoes a longer or shorter period of rest;[1] in some seeds the endosperm and perisperm (especially the latter) may be wanting. The life-history of *Pinus* is shown in tabular outline on p. 434 and in diagram in figure 310.

Comparison with Fern and Little-club-moss.—Anatomical structures that have the same anatomical or morphological value in the structure of the organism are *homologous;* structures that perform the same functions (without reference to their *homology*) are *analogous.* The following table indicates the homologies between fern, little-club-moss, pine, and clover (Table IX). From a study of this table the seeds of the pine tree and the clover may be interpreted in the light of the structures so clearly differentiated and distinct in the fern and little-club-moss.[2] It will be recognized at once that a seed cannot really be understood or interpreted unless one knows, in broad outlines at least, the life history of some of the lower plants, such as the fern and its relatives.

It is not necessary thus to understand the structure of a flower and a seed in order to raise good crops by planting seeds; it is necessary, however, if one wishes to be intelligent, beyond the economic demands of his vocation, concerning the materials with which he works—if he wishes his intellectual life to be enriched as much as possible, his mental horizon to be widened, his pleasures to become more than physical by the vocation he follows.

[1] In some seeds the embryo is capable of resuming growth (*i.e.*, the seed will "germinate") after a resting period of from one to several years; in other species, such for example as the mangrove, the embryo appears to have no resting period, but continues its growth uninterruptedly—that is, the seed "germinates" as soon as it is mature. Cf. p. 153, foot note.

[2] Cf. pages 11 and 423–424.

TABLE IX

Structure	Fern	Little-club-moss	Pine	Clover
SPOROPHYTE	Fern Plant	Plant body	Pine tree	Clover Plant
Foliage Leaf	Foliage leaf	Green scale	Pine "needle"	Compound Leaf
Inflorescence	.....	Cone	Cones, ♂ and ♀	"Blossom"
Flower	.....	.....	.....	**Flower**
Sporophyll	Frond	Sporophyll	Ovule-bearing scale	
Sporangium	Sporangium			
Microsporophyll	.....	Microsporophyll	Scale of male cone	Stamen
Microsporangium	.....	Microsporangium	Anther	Anther
Megasporophyll	.....	Megasporophyll	Scale of Carpellate Cone	Carpel of Pistil
Megasporangium	.....	Megasporangium	Ovule (nucellus)	Ovule (nucellus)
Oösperm	*Oösperm*	*Oösperm*	*Oösperm*	*Oösperm*
Embryo	*Embryo*	*Embryo*	*Embryo*	*Embryo*
Resting embryo	.....	.....	**Resting Embryo**	**Resting Embryo**
Seed-coat	.....	.....	Seed-coat	Seed-coat
Seed	.....	"Near-seed"	**Seed**	**Seed**
GAMETOPHYTE	Prothallus			
Microspore	.....	Microspore	Young pollen grain	Young pollen grain
Male Gametophyte		Mature Microspore	Mature pollen grain	Mature pollen grain
Pollen Tube	.....	.....	Pollen-tube	Pollen-tube
Antheridium	Antheridium	Antheridium	Cell	
Sperm	*Sperm* (motile)	*Sperm* (motile)	*Sperm*-cell	*Sperm*-cell
Megaspore	.....	Megaspore	Megaspore	Megaspore
Female Gametophyte	.....	Female prothallus	Endosperm	Embryo-sac
Archegonium	Archegonium	Archegonium	Archegonium	
Egg	Egg	Egg	Egg	Egg

CHAPTER XXI

LOWER CRYPTOGAMS

The lower cryptogams, that is, those below the ferns in the scale of life, have little known importance for agriculture, except the fungi and bacteria. In order to understand the fungi and bacteria, a knowledge of the algae is helpful, and the natural transition from ferns to algae is through the mosses and liverworts. We will, therefore, pass these three forms—mosses, liverworts, and algae—briefly in review as the most logical approach to the other two.

MOSSES

The Mosses are divided into three main groups or *orders, viz.*

1. **Bryales** (the true mosses).
2. **Andreaeales** (the black mosses)
3. **Sphagnales** (the peat-mosses)

LIFE HISTORY OF A TRUE MOSS

For illustration we will choose the common, widely-distributed, hair-cap moss, *Polytrichum commune,* belonging to the Bryales.

There are two types of plant-body. Both consist of an unbranched axis, bearing delicate, pointed, green foliage-leaves. At the apex of one type is a rosette of scale-like, pointed leaves, quite distinct in appearance from the foliage leaves. Examination within this rosette discloses a group of club-shaped antherida, each bearing numerous sperms, motile by means of *two* cilia. This plant will, therefore, be recognized as a leafy, male gametophyte (Fig. 311). Often, by *proliferation,* a second moss plant grows out from the tip of the older one, its base surrounded by the antheridia.

At the apex of the other type, when maturing, are found numerous bottle-shaped organs, which, on closer examination, are found to be long-necked, stalked archegonia, bearing eggs in

their venters. After fertilization the oösperm develops a long, slender stalk or *seta*, bearing at its upper end a spore-case. This

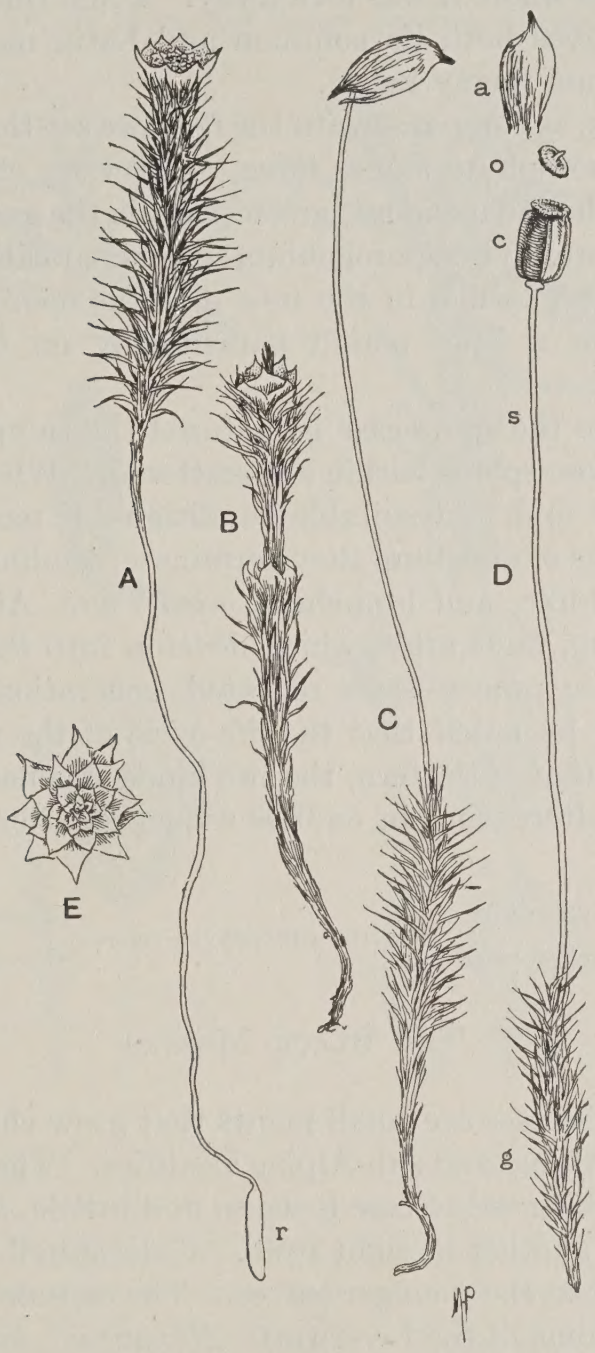


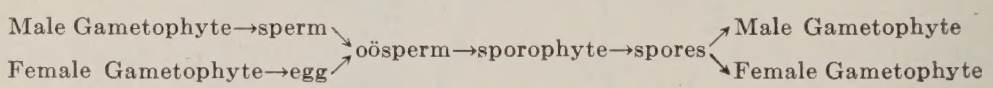
FIG. 311.—Hair-cap moss (*Polytrichum commune*). *A*, male plant; *B*, same, proliferating; *C*, female plant, bearing sporogonium; *D*, same; *g*, gametophyte; *s*, seta; *c*, capsule; *o*, operculum; *a*, calyptra, *E*, top view of male plant.

is the sporophyte phase of the moss; because of its simplicity it is often called a *sporogonium*. As the seta elongates it carries

up the dried archegonium, which appears as a brown, membranous cap (the *calyptra*) fitting over the spore-case, and fringed along the edge where it was torn away. From this latter feature the moss derives both its common and Latin names—hair-cap and *Polytrichum* (many hairs).

In the moss, as compared with the fern, we see that the gametophyte and sporophyte stages have, as it were, changed places. In the moss the independent, green plant is the gametophyte, on which the sporophyte (sporogonium) grows parasitically throughout its existence, while in the fern it is the sporophyte that *at first* grows for a brief period parasitically on the ephemeral gametophyte.

By the time the spore-case is matured the calyptra has fallen off and the loose spores within are scattered. When they fall on moist ground and find suitable conditions of temperature and light, as well as of moisture, they germinate, sending out a slender green, thread-like, and branching *protonema*. At intervals, on the protonema, buds arise, which develop into the leafy sporophytes. These processes are repeated, generation after generation. It will be noted that the life-cycle of the moss is of the same type as that of the fern, the two kinds of generations, sexual and asexual, alternating in endless sequence, after the following formula:



The Black Mosses

The Black Mosses are small plants that grow chiefly on rocks, especially in Alpine and sub-Alpine localities. The dark colored, black, or blackish red foliage is dense and brittle, and the leaves fold over one another in eight rows. Chlorophyll appears to be lacking except in the younger leaves. The capsule opens by four valves, as in some of the Liverworts (*Hepaticae*), and it is largely on the basis of this character (absent in other mosses) that the Black Mosses have been placed in an order by themselves. The spores, on germinating, give rise to a somewhat flattented protonema. The order (*Andreaeales*) contains but one genus, with several species.

The Peat Mosses

Like the *Andreaeales*, the *Sphagnales* contain but one genus, *Sphagnum*, of which there are many species; forty are native of

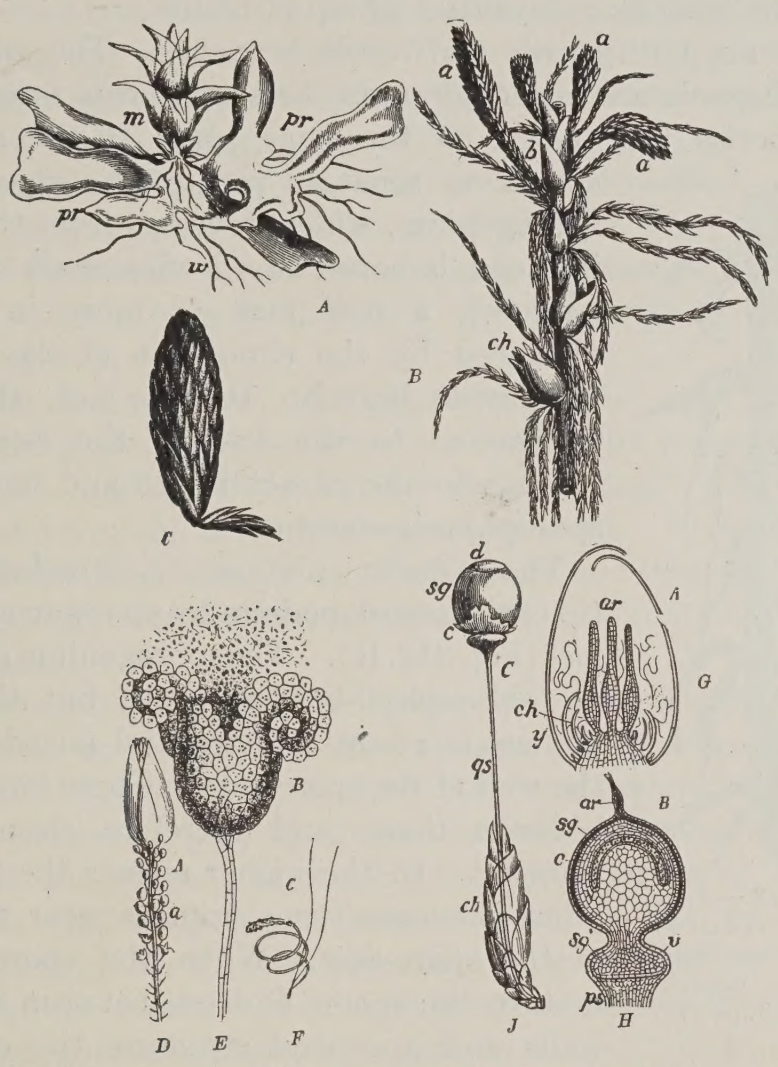


Fig. 312.—*Sphagnum acutifolium.* *A*, prothallus (*pr*), with a young leafy branch just developing from it; *B*, portion of a leafy plant; *a*, male cones; *ch*, female branches; *C*, male branch or cone, enlarged with a portion of the leaves removed so as to disclose the antheridia; *E*, antheridium discharging spores; *F*, a single sperm; *G*, longitudinal section of a female branch, showing the archegonia (*ar*); *H*, longitudinal section through a sporogonium; sg^1, the foot; *ps*, pseudopodium; *c*, calyptra; *sg*, sporogonium, with dome of sporogenous tissue; *ar*, old neck of the archegonium; *J*. *Sphagnum squarrosum; d*, operculum; *c*, remains of calyptra; *qs*, mature pseudopodium; *ch*, perichaetium. (From Schimper.)

North America—all of them wholly or partially aquatic. In proceeding from the True Mosses to the more primitive Peat Mosses it is interesting to note that we pass from forms having a

tubular protonema (in *Bryales*) to those having a flattened protonema (in *Andreaeales*), and thence to the *Sphagnales* with a protonema which is a flat thallus (Fig. 312), resembling, in this and other characters, the plant body of some of the lower Liverworts, the next more primitive group of plants.

There are both sterile and fertile branches. The antheridia and archegonia are never borne on the same fertile branch. In some species they occur on the same plant (*monoecious*), in others on separate plants (*dioecious*). The sporogonium, which develops from the fertilized egg, is borne on a leafless stalk (pseudopodium), a half inch or more in length, produced by the elongation of the apex of the fertile branch. It does not, therefore, correspond to the seta of the Bryales; it belongs to the gametophyte and not to the sporophyte generation.

FIG. 313.—*Sphagnum cuspidatum*, showing innovation, or short, branches. (After Schimper.)

The globular spore-case is attached to the tip of the pseudopodium by an organ called the *foot* (Fig. 312, H). The sporogonium possesses no chlorophyll-bearing cells, but there are numerous groups of stomatal guard-cells on the wall of the spore-case. These have no slit between them, and therefore stomata are wanting. In the higher mosses the sporogonium possesses true stomata near the base of the spore-case. When the spore-case is mature the spores lie loose between its outer walls and a central structure the *columella* (little column).

The spore-case opens by means of an apical lid (operculum), as in the *Bryales*, thus allowing the dry spores to escape and be carried away by the wind.

The plants are perennial by means of the sterile branches which become established as new plants as the older plants die off. Under favorable conditions young plantlets, called *innovation branches*, may develop on the sterile branches at the tip and back from the tip, and become established as independent plants (Fig. 313).

There are no fibro-vascular bundles in the stem and, correlated with this, is the absence of a mid-rib and veins in the leaves. At the bases of the leaves are glandular hairs, and, as the leaves mature, the protoplasm of part of their cells becomes entirely transformed into thick cell-walls, leaving the cell-cavity empty of everything but air and water. These empty cells greatly mask the smaller ones containing chlorophyll, and this accounts for the pale color of the plants.

The walls of the empty cells are usually perforated with numerous pores, and a similar kind of cell also develops in the outer tissue of the stem. These cells are very hygroscopic, and rapidly absorb water in large quantities so that the entire living plant is saturated with water.

By the death of the older plants year after year a stratified deposit of plant tissue is formed, including the remains of other bog-plants, and thus are formed the peat bogs, which, in the course of centuries, may become level pastures. In the decomposition of the plants quantities of humic acid and tannin are formed, which preserve for centuries plant and animal remains imbedded in the peat.

Economic Importance of Sphagnum.—Dried sphagnum has long been used by nurserymen and florists for packing plants for shipment. In certain parts of Scotland and Ireland the peasants depend almost entirely upon peat for fuel, and there are billions of cubic feet of peat in the United States in easily accessible localities, that might be utilized whenever needed, for fuel. In cities Sphagnum is often used instead of straw as bedding for horses.

During the World War sphagnum became recognized as affording a valuable substitute for cotton in surgical dressings. This value is owing to its hygroscopic character. Large quantities of it were used by the British Red Cross, and it has been considered by some superior to cotton as a surgical dressing, since it absorbs more rapidly, takes up greater quantities of liquid per unit weight of dressing, and retains the liquids better so that dressings do not have to be changed so often. It is also cooler and cheaper than cotton. Sphagnum has been adopted by the American Red Cross as a surgical dressing. Certain species are much better than others, while some species are quite unsuited to this purpose.

The use of Sphagnum in surgery affords a striking illustration of the value of research in pure science even when no practical application of the knowledge can be foreseen. Years ago botanists began to study Sphagnum moss just because it interested them as a plant. They studied its structure, life history, and distribution from purely scientific interest. There was no thought as to any possible use of this knowledge except as it threw light upon our knowledge of the history of plants, and upon certain geological processes as in the formation of bogs and meadows, and the obliteration of lakes. Then came the crisis of the World War and all of this knowledge became of the highest importance. The alleviation of suffering and the saving of lives became dependent upon someone being able to recognize the the various species of Sphagnum, and knowing the location of large deposits of the valuable species. It is always worth while to pursue knowledge for its own sake—as an end in itself.[1]

LIFE HISTORY OF A LIVERWORT

The next group of plants more simply organized than the mosses are the Liverworts. They are widely distributed, as to climate and habitat, in tropical and temperate regions—some aquatic forms submerged, others floating, some growing on other plants (epiphytes), some in arid situations. Most species, however, prefer a moist situation, and this fact, combined with the need of water for fertilization by motile sperms, indicates descent from aquatic ancestors.

One of the commonest forms is *Marchantia polymorpha.*[2] The plant body is a branched, green thallus that is not differentiated into root and shoot. The undersurface of the thallus bears numerous thread-like structures which hold the plant in place, and absorb water and dissolved substances from the soil. They

[1] Another and much more important illustration of the value of research in pure science has been afforded by the discovery of the part played by the mosquito in the spread of yellow fever and malaria, and of other insects—*e.g.*, the louse and the Tse-tse fly—in the spread of other infectious diseases. Fifty years ago nothing would have seemed further removed from the important practical needs of our daily lives than a knowledge of the structure, habits, and classification of mosquitoes.

[2] Named from Nicholas Marchant (died 1678), a French botanist, by his son, Jean (1650?–1738), also a botanist.

FIG. 314.—*Marchantia polymorpha.* Male plant, bearing antheridiophores. (After Atkinson.)

FIG. 315.—*Marchantia polymorpha.* Female plant, bearing archegoniophores. (After Atkinson.)

are not true roots, but, since they function as roots, they are called *rhizoids* (root-like). Some of the plants bear somewhat flat, lobed discs raised on a slender stalk. Imbedded in the tissues of the disc are numerous antheridia, opening to the surface. Since these structures bear antherida they are called *antheridiophores* (Fig. 314). If a drop of water is placed on the slightly concave upper surface of the disc where the sperms are mature they will swim out into the water in such numbers as to give it a milky appearance.

Other plants bear odd looking structures that remind one of a tiny, many-rayed green starfish, raised high on slender stalks (Fig. 315). The under surface of these structures bears archegonia surrounded by delicate membranes. Fertilization takes

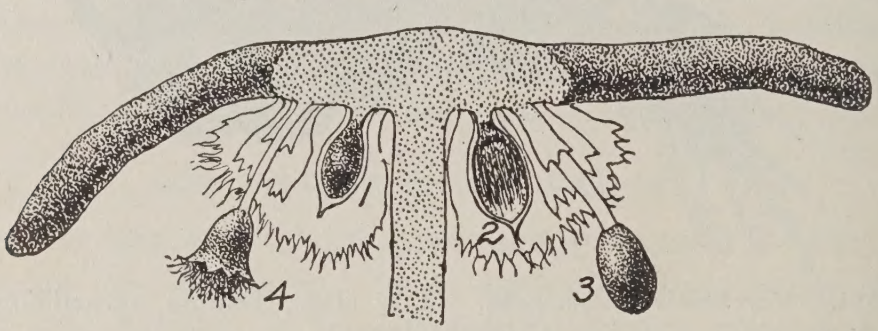


FIG. 316.—*Marchantia polymorpha.* Section of archegonial receptacle showing ripe sporogonia (sporophytes). The capsule of one at the left has opened, scattering spores; two are still enclosed in the wall of the archegonium. (After Atkinson.)

place before the stalks have elongated enough to raise the archegonial receptacles or *archegoniophores* above the surface of the thallus. The sperms require free water, and swim by their own efforts from the male to the female plants, and into the archegonia, where they fuse with the eggs. A fertilized egg produces a stalked spore-case, known as a *sporogonium*—in reality a simply organized sporophyte (Fig. 316). The spores fall to the ground, and under suitable conditions of temperature, light, and moisture, they germinate, giving rise, some of them to antheridial or male gametophytes, others to archegonial or female gametophytes. As in the case of moss, fern, little-club-moss, pine, and clover (and other plants), we have the continuous alternation of sexual with asexual generations, after the following formula:

Sporophyte→spore ↗ Male gametophyte→sperm ↘
                 ↘ Female gametophyte→egg ↗ oösperm→Etc.

Vegetative multiplication may result from a portion of the thallus establishing itself independently, or from the development of the numerous "brood-buds" or *gemmae*, borne in small cupules on the upper surface of the thallus (Fig. 196).

ALGAE

Next below the liverworts are the Algae. The name, *Alga*, is the Latin word for seaweed. Not all of the algae live in the sea, but many of them do; others live in fresh water, and still others require only moist situations on land—growing on the soil, on the trunks of trees, on stones and fences, or on the surfaces of flower pots in greenhouses. Some forms live in the tissues of liverworts, in the stems of cycads, or even in the tissue of certain animals, such, for, example, as the green hydra (a diminutive relative of the coral), common in fresh water ponds.

Economic Uses.—Many marine algae are of great economic importance—such as the "Irish moss," a Red alga (*Chondrus crispus*), the source of "seamoss farine;" dulse (*Rhodymenia*); and certain kelps (*Laminariaceae* and *Fucaceae*), to be mentioned later. Agar-agar (or simply agar), so extensively used in biological laboratories as a culture medium for fungi, bacteria, and other plants, is a gel derived from varieties of *Gelidia* and other Red Algae common in Ceylon, Java, and Madagascar.

The green algae are of considerable economic importance in the soil. Since they possess chlorophyll, they manufacture in sunlight quantities of sugar and starch, and thus are believed to favor the development of nitrogen bacteria, such as *Azotobacter* and others, that depend on the presence of such nutrients. Herein, it is claimed, lies the advantage of allowing land to lie fallow: the algae develop in the upper layers of the soil, this promotes the growth of bacteria, and thus increases the nitrogen content.

Algae are one of the sources of contamination of drinking water, and they may also become a nuisance in ponds and lakes, especially in city parks. Both Blue-green and Green Algae are involved. The Blue-greens produce an oil which may give a bad odor and taste to drinking water. Among the Green Algae the unicellular *Diatoms* often cause trouble, giving the water an unpleasant taste and also an odor resembling fish. The Pond Scum (*Spirogyra*) is at times a source of trouble by overgrowing

beds of watercress and killing the young plants. The *Synura*, which gives to water an odor of ripe cucumbers, and was particularly noticeable in the water supply of New York City in 1922, belongs to a group of *Flagellates*—organisms on the border line between the plant and animal kingdoms, though commonly considered as animals.

It has been found that copper sulphate in highly dilute solution is very poisonous to algae, and by treating the water of ponds and reservoirs with relatively small quantities of that salt the algae may be reduced or eliminated with more or less success.

Classification.—The Algae, according to color, fall naturally into four main groups, as follows, proceeding from the more highly organized to the simpler forms:

Red algae (*Rhodophyceae*)
Brown algae (*Phaeophyceae*)
Green algae (*Chlorophyceae*)
Blue-green algae (*Cyanophyceae*)

Associated with these differences in color are certain anatomical differences which also lead to a similar grouping.

1. *Red Algae.*—Nearly all species are marine, and grow attached. Asexual reproduction is by means of spores, while sexual reproduction results by the fusion of male and female cells or gametes. Chlorophyll is present, but is masked by the red coloring matter. *Nemalion* may be cited as an example (Fig. 317).

2. *Brown Algae.*—All but a few rare species are marine. As in the Red algae, chlorophyll is present, but is masked by the brown coloring matter. All forms grow attached to rocks, piles, or other supports; they attain their greatest size in the cooler water of the subarctic seas. Various statements have been made in the literature of botany and of exploration concerning the size of these plants, especially of the *giant kelps* (Fig. 318). Kjellman[1] gives the maximum length of one of these kelps (*Nereocystis leutkeana*) as 100 meters, though he does not name the locality where the specimen was found. Even greater

[1] Kjellman, F. R. Laminariaceae. Engler and Prantl, Die Natürlichen Pflanzenfamilien. **12**: 259. 1897. Harvey, W. H. (Nereis Boreali Americana. Part I, p. 82. Smithsonian Institution. 1852) reported a maximum length of 103 meters.

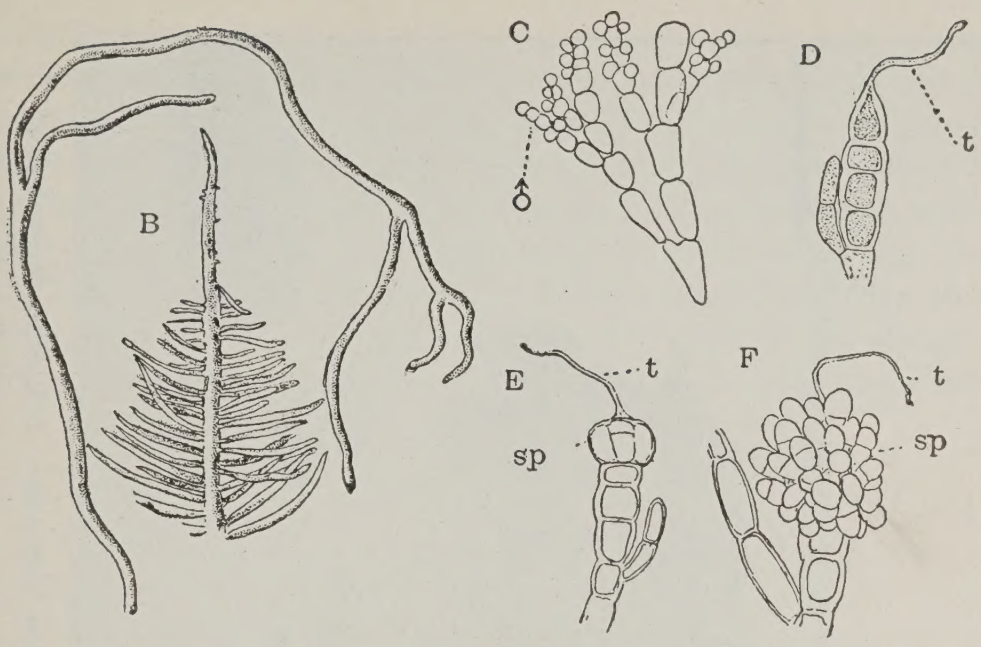


FIG. 317.—Red algae, sometimes called Thread-weeds. A, C-E, *Nemalion multifidum* (natural size); B, *N. Andersonii* (natural size); C, branch bearing oögonium (carpogonium), with enlarged base and slender neck or *trichogyne* (*t*). E, young sporocarp or spore-fruit (*sp*), with the neck withering; F, older (much branched) sporocarp (*sp*). (After Campbell.)

FIG. 318.—A giant Kelp, one of the Brown Seaweeds. (Courtesy U. S. D. A. Bur. Soils.)

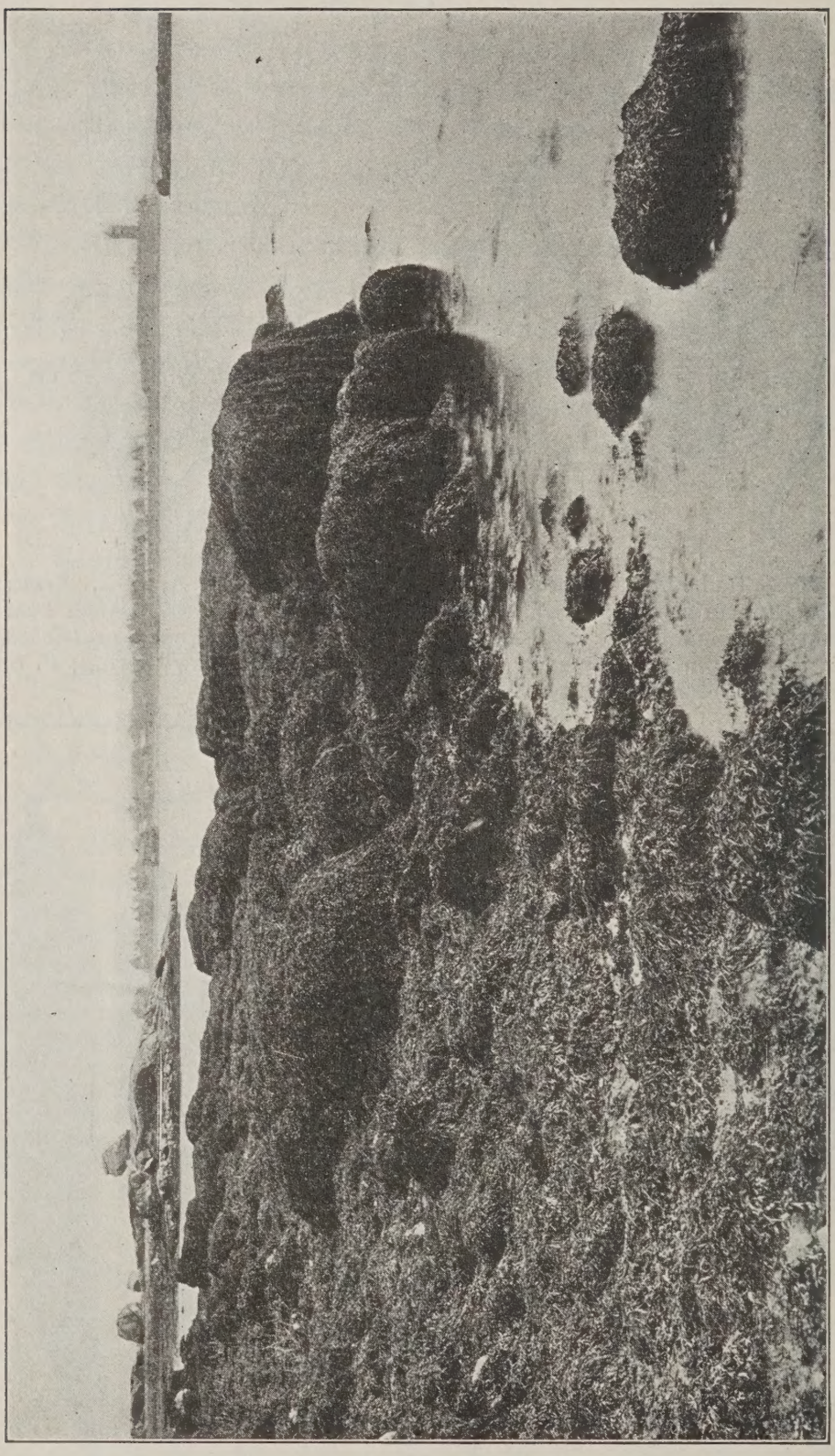


FIG. 319.—*Ascophyllum nodosum*, and *Fucus*. Hunter's Island, New York City. (Photo by M. A. Howe.)

lengths have been reported,[1] but more recent and careful measurements of specimens collected at various points along the east coast of the Pacific, from Alaska to Pacific Grove, California, failed to disclose any specimens of *Nereocystis* more than 38.4 meters long. Kjellman also reported a maximum length of 200–300 meters for *Macrocystis*, but the largest specimens found by Frye and others in the Puget Sound region were only 40 feet long, and on the Californian coast, 45.7 meters, or about 150 feet.[1] Species of the Antarctic *Lessonia*, though true thalli,

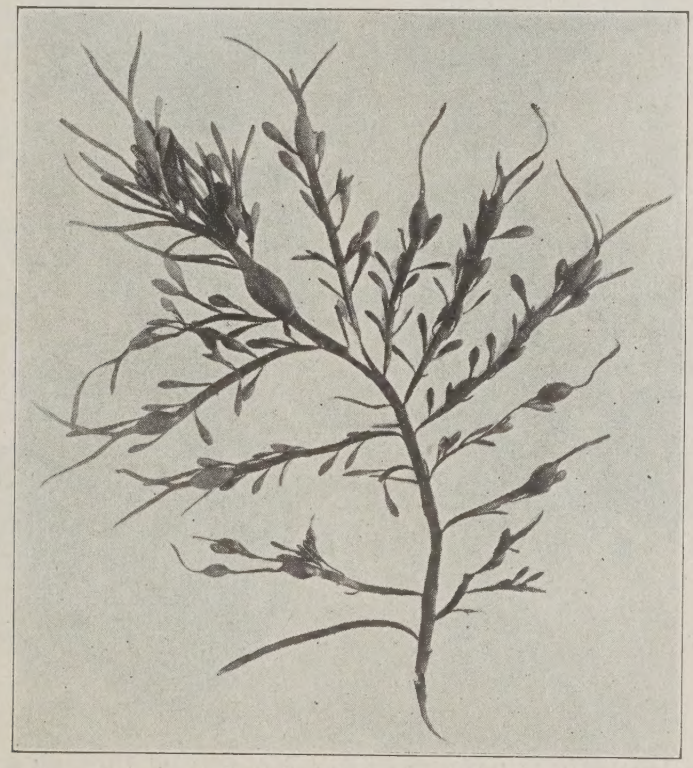


FIG. 320.—Portion of plant of *Ascophyllum nodosum*. × ⅜.

have a main stalk as large as one's arm, several yards high, and assume tree-like proportions with their numerous branches.

Two of the commonest forms in the North Atlantic are the Rockweeds, *Ascophyllum* and *Fucus* (Fig. 319). The swollen tips (*receptacles*) of the thallus (Fig. 320) contain numerous cavities or *conceptacles*, opening to the surface. In the conceptacles are borne numerous antheridia and simple egg-bearing organs called *oögonia*, which perform the function of archegonia,

[1] Frye, Rigg, and Crandall. The size of kelps on the Pacific coast of North America. Bot. Gaz. **60**: 473–482. Dec., 1915.

though of much simpler structure than the latter. When the gametes are mature the eggs float out and the sperms swim out into the water, where fertilization takes place. The difference in size between egg and sperm is greater than in any other known species of plant (Figs. 321 and 322).

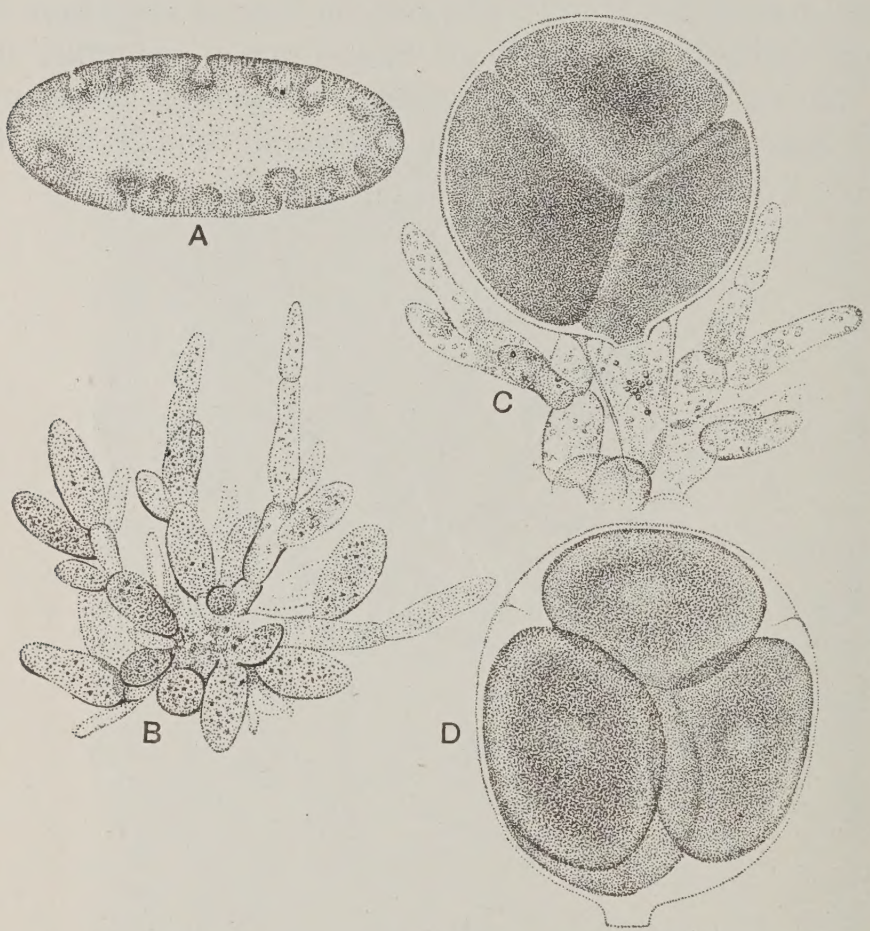


FIG. 321.—*Ascophyllum nodosum.* *A*, Cross-section through a female receptacle; *B*, spermagonia; *C*, ripe oögonium; *D*, eggs, freed from the oögonium, but still enclosed by the separated inner layer of the oögonial wall. (Redrawn from Thuret and Bornet.)

Kelps as Fertilizer.—Commercial fertilizers comprise three classes of materials:

1. Superphosphate, which is the basis of commercial fertilizers in all countries;

2. Nitrogen carriers, the most important of which is sodium nitrate or Chile saltpeter;

3. Potash carriers, the salts of potassium.

Hitherto the world's chief inorganic source of soluble potash salts has been the mines at Strassfurt and the Magdeburg-Halberstadt region of Germany, and the United States has been largely dependent upon these mines, consuming about one fifth of their entire output. But this country has a promising source

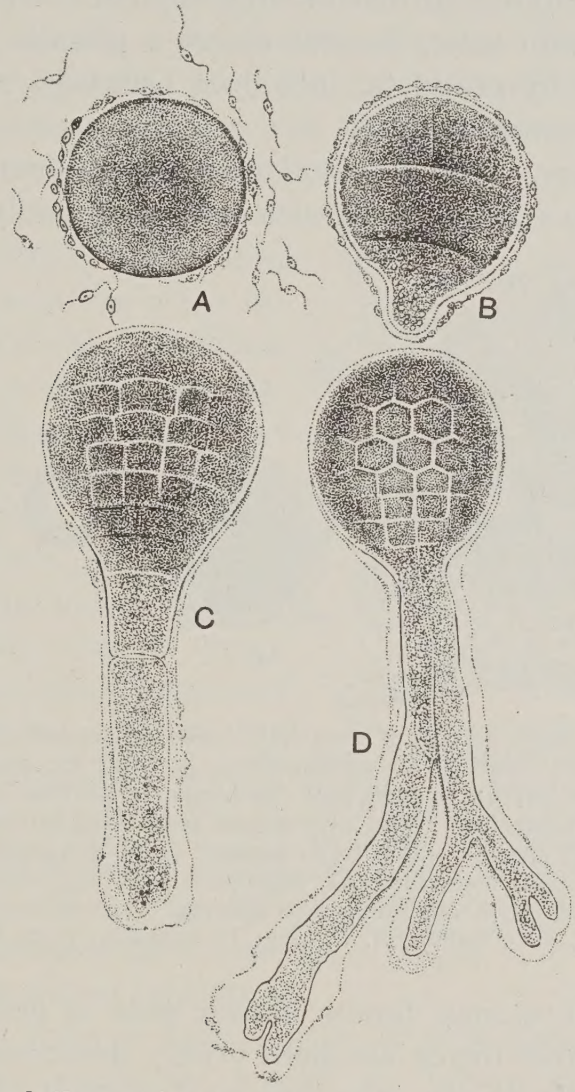


FIG. 322.—*Ascophyllum nodosum.* *A*, egg at the time of fertilization, surrounded by numerous sperms. × about 200; *B*, oösperm germinating, 6 days old; *C*, *D*, somewhat older stages than *B*. (Redrawn from Thuret and Bornet.)

of potash fertilizer in the so-called "Kelp groves" along the Pacific coast. Some of the groves or beds occupy an area of more than 25 square miles.

The fertilizing value of kelps has long been known, and those from the Pacific coast of America have five or six times higher

percentage of potash than those on the Atlantic coast, and more than those of Japan where they are extensively used. Surveys made by the U. S. Department of Agriculture disclosed the existence of many millions of tons of kelps (*Nereocystis luetkeana*, *Macrocystis pyrifera*, and others).[1] It has been estimated that one ton of thoroughly air-dried kelp will yield at least 500 pounds of pure potassium salts, besides about 3 pounds of iodine and other valuable by-products, including cellulose, algin, and the sugars dextrine and mannite.

3. *Green Algae.*—The *Chlorophyceae* are the commonest kind of algae in fresh water. They also occur commonly on the moist

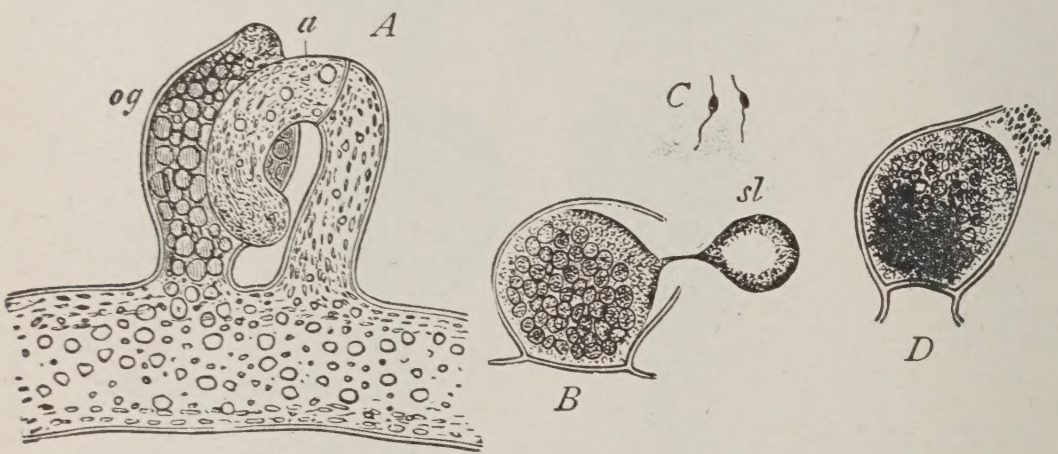


FIG. 323.—*Vaucheria sessilis* (Green-felt). Sexual reproduction. *A*, portion of a green filament bearing an antheridium (*a*) and an oögonium (*og*); *B*, a mature oögonium having opened and discharged a portion of its protoplasm, preparatory to fertilization. The protoplasm remaining in the oögonium is the egg-cell or egg. *C*, sperms which have escaped from the antheridium by swimming by means of their two cilia. *D*, oögonium with egg about to be fertilized by the sperms which have collected at the opening. (*A*, *B*, *D*, × about 100; *C* × about 350. *A*, *D*, after Sachs; *B*, *C*, after Pringsheim, from Barnes.)

surfaces of soil, stones, fences, flower pots in greenhouses, and elsewhere. Three forms are here briefly described to illustrate the progressively simple structure and method of reproduction met with as one passes from the more highly organized to the one-celled forms.

a. *Vaucheria terrestris*, commonly known as "green felt." This, and other species of *Vaucheria*, are specially common on

[1] On kelps as fertilizers see Cameron, Frank K., and others. A preliminary report on the fertilizer resources of the United States. 62nd Congress, 2d session. Senate Document No. 190. Washington, 1912. pp. 40, *et seq.*

surfaces of soil and flower pots, but certain species also occur floating. The plant body consists of a slender, green filament, not divided into cells by cross-walls. On this account the numerous nuclei are distributed in one continuous mass of protoplasm; such a structure is called a *coenocyte* (communal cell). The only exception to the general absence of cross-walls is in the formation of the reproductive organs. These consist of short branches, separated from the vegetative filament by cross-walls. As is shown in figure 323, the protoplasm of certain of these branches develops into motile sperms, and these branches are, therefore, antheridia; the protoplasm in the other reproductive branches becomes organized into a single large egg. After fertilization the egg, or oösperm, develops into another plant. In asexual reproduction the protoplasmic contents at the tip of a branch (separated from the main branch by a cross-wall) become organized into a single, large, green motile spore (swarmspore), which swims away and, after a longer or shorter period of rest develops into a new individual (Figs. 323 and 324). Because of the formation of tubes in sexual reproduction *Vaucheria* belongs to the order of tube-algae (*Siphonales*).

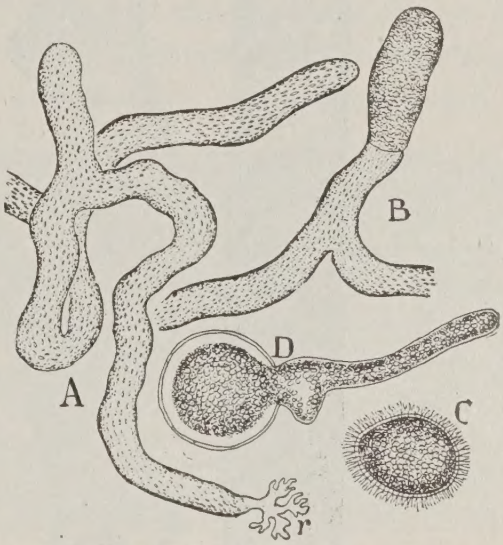


FIG. 324.—*Vaucheria* sp. *A*, portion of the branching, green filament, having a root-like organ or "holdfast." At *B* an end of a filament is enlarging to form a zoöspore. *C*, zoöspore, showing the numerous cilia by which it swims through the water. *D*, germination of a zoöspore. (After C. C. Curtis.)

b. *Spirogyra*, commonly known as "green silk" (from its slippery feel), or as "pond scum," grows floating at various depths. In bright, sunshiny weather the bubbles of gas given off by the green filaments in connection with photosynthesis, give the mass of filaments a buoyancy and carry it up to the surface. From its delicately foamy appearance at such times it is often called "frog-spittle." *Spirogyra* belongs to the class of conjugate algae (*Conjugatae*), so named because of the habit

of the filaments of becoming "yoked" together, *conjugation*, in reproduction.

The plant body is a thread-like, bright green filament of uniform diameter, *separated by cross-walls* into many cells (Fig. 325).

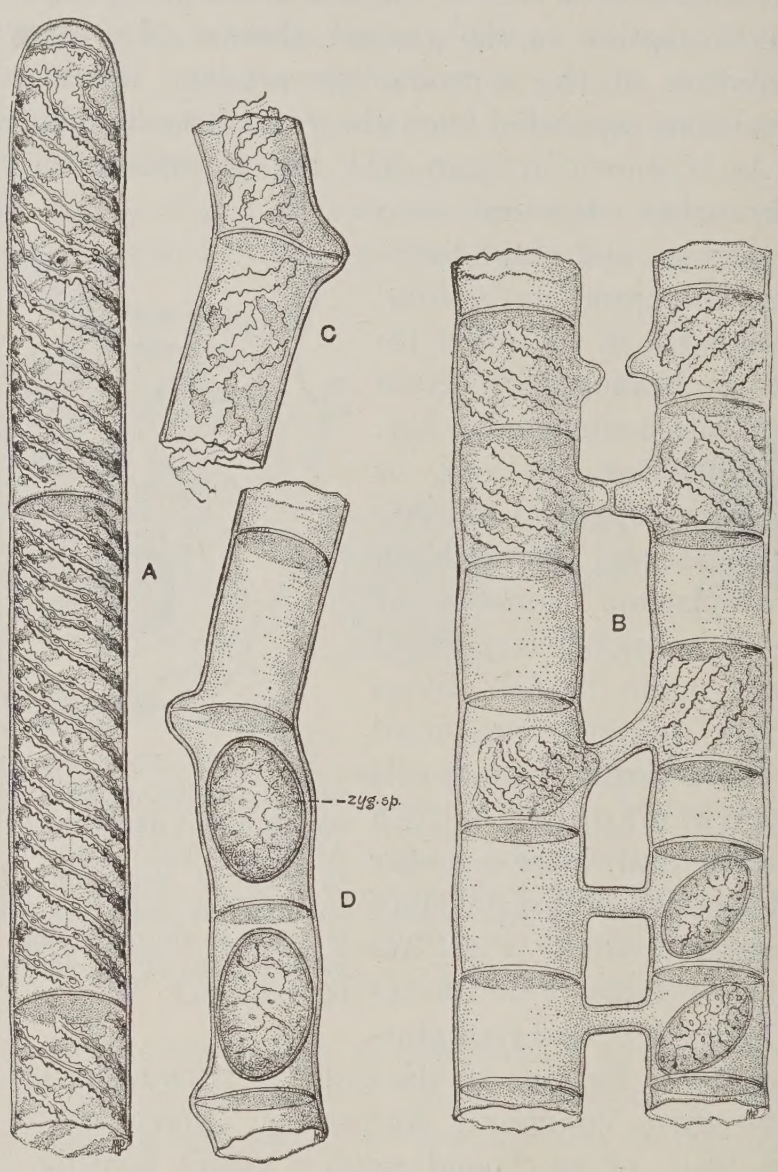


FIG. 325.—*Spirogyra* sp. *A*, terminal portion of vegetative filament; *B*, stages of scalariform conjugation; *C*, preparation for lateral conjugation; *D*, zygospores formed by lateral conjugation. *Cf.* Fig. 326.

In each cell there are from one to two or more large ribbon-like chloroplasts or *chromatophores*, arranged like a spiral against the inner surface of the cell, whence the name, *Spirogyra*. The chromatophores grow as the cell grows, and divide when the

cell divides. Imbedded in them at inervals are refractive protein bodies called, from their shape, *pyrenoids* (from the Greek, *pyren*, a kernel, and *eidos*, resembling). These are starch formers, and are commonly surrounded by small grains of starch. They are smaller in supplying than in receiving gametes, and are connected by strands of cytoplasm with the cytoplasm surrounding the nucleus. Pyrenoids have been found in the plant world only in Algae and in the Liverwort, *Anthroceros*.

In sexual reproduction the tips of lateral branches (or tubes) from adjacent filaments meet and fuse, and the contents of one of the cells—the *supplying gamete*—pass through this connecting tube and fuse with the protoplast in the other, or *receiving gamete*.

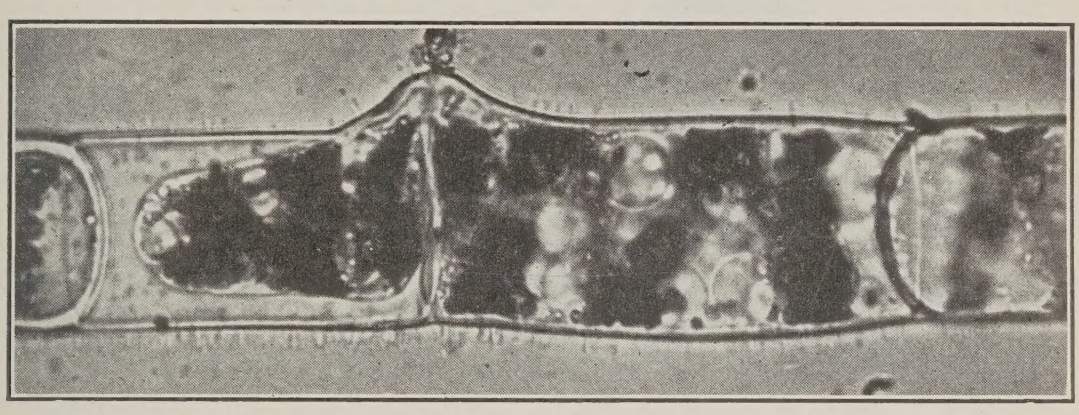


FIG. 326.—*Spirogyra longata*. Portion of a monoecious filament showing two adjacent cells in the early stages of conjugation. This type of conjugation is called *lateral*. Ladder-like or *scalariform* conjugation of dioecious filaments is shown in figure 325. Note the pulsating or *contractile vacuoles*. (After Lloyd.)

In some species conjugation takes place between adjacent cells of the same filament. The presence of *contractile vacuoles* in conjugating *Spirogya* (Fig. 326), and their function in moving the protoplasts of the supplying gamete over into the cell-cavity of the receiving gamete in conjugation, is noted on p. 19. The protoplasmic mass that results from this conjugation becomes surrounded by a thick cell-wall of its own, and is rich in nourishment; it is termed a *zygospore*. The zygospore commonly rests before it germinates, and thus is able to tide the species over periods of winter or of prolonged drought.

c. *Pleurococcus*.—The simplest type of green algae is illustrated by *Pleurococcus*, commonly found on the moist surfaces of tree trunks, rocks, boards, and other objects. The plant body con-

sists of a single globular, green cell. Reproduction takes place only by cell-division. Often the cells thus formed adhere for a longer or shorter period, giving rise to a pseudo-multicellular

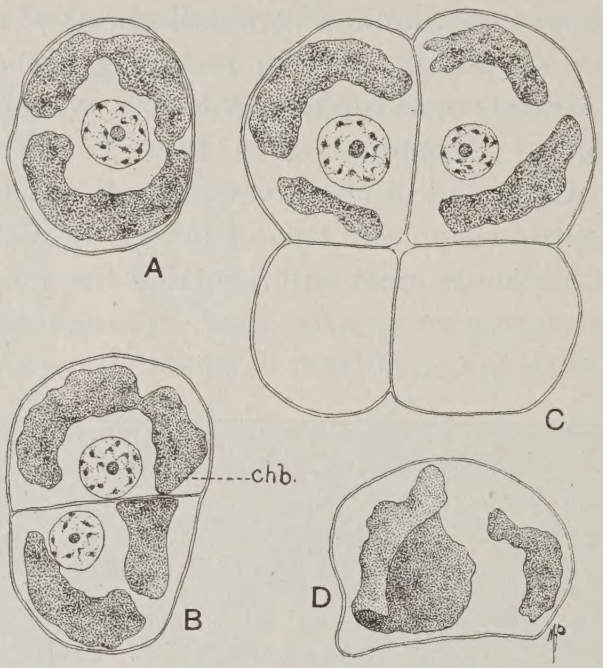


FIG. 327.—*Pleurococcus vulgaris*. Sections of one-, two-, and four-celled plants, showing the nuclei and the large chlorophyll bodies (*chb*) to which the green color of the plants is due. In *D*, the larger chloroplast is shown in perspective. (Camera lucida drawings from a microscopic preparation by E. W. Olive.)

plant body (Fig. 327). Sexual reproduction is unknown. The simple life history of the plant is indicated in the following outline:

OUTLINE OF LIFE HISTORY OF PLEUROCOCCUS

Unicellular plant
↓
Cell-divisions
↓
Temporary cell-aggregates
↓
Separation of daughter-cells
↓ ↓ ↓ ↓
Unicellular plant | Unicellular plant | Unicellular plant | Unicellular plant

In *Pleurococcus* the green plant is reduced almost to its lowest terms. There are no organs, except those common to every green cell. Every essential function is performed by the one

cell—absorption, photosynthesis, digestion, assimilation, growth, respiration, and reproduction. In other words, *Pleurococcus* is a generalized plant, with almost no division of physiological labor.

4. *Blue-green Algae.*—This group, the *Cyanophyceae* ("blue-greens") are among the very simplest of plants containing chlorophyll. There is no nuclear membrane; the nuclear substance and also the *phycocyanin* and chlorophyll are distributed in the protoplasmic mass of the cell,—true nuclei and chromoplastids being absent. The plant body is a single cell, or a *cell-plate* (superficial aggregate of cells), or a filament (linear aggregate of cells). Reproduction takes place only by cell-division, and by the breaking up of the plates or filaments into smaller pieces.

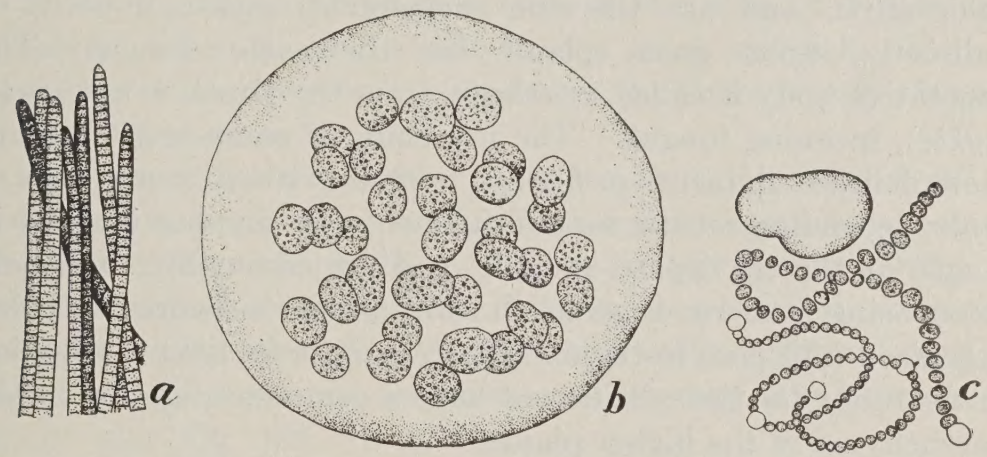


FIG. 328.—Blue-green algae. *a*, *Oscilatoria violacea* (After Tilden) *b*, *Gleocapsa gigas* (After W. and G. S. West); *c*, *Nostoc pruniforme;* colony (above) and filaments. (After Cooke.)

Sexual reproduction (by cell-fusion) is unknown. These plants appear to be closely related to the bacteria (See p. 516). Common illustrations of the blue-greens are species of *Gloeocapsa*, *Nostoc*, and *Oscillatoria* (Fig. 328). Some species of *Nostoc* live in the root-nodule tissues of *Cycas revoluta* (p. 212), and in the tissues of certain liverworts (*e.g.*, *Anthoceros*). *Oscillatoria* is a fascinating plant to observe under the microscope because the slender, septate filaments are continually oscillating, like miniature pendulums, whence the name, *Oscillatoria.* This plant is commonly found as a purplish or bluish-green coating on the surface of flower pots and elsewhere in damp greenhouses.

The lower cryptogams include, also, the fungi, to be discussed in the next chapter.

CHAPTER XXII

CHARACTER AND LIFE HISTORIES OF FUNGI

What is a Fungus?—The word *fungus* (plural, *fungi*) is the Latin name for mushroom. As noted in the preceding chapter, fungi are cryptogams or plants that reproduce by spores but never by seeds. They differ from other cryptogams in having no chlorophyll, and are therefore dependent, either directly or indirectly, upon green plants for their nourishment. The vegetative body is called *mycelium*, from the Greek word (μυκής, *mykēs*), meaning fungus. The mycelium is composed of one or more delicate filaments or *hyphae*, with or without cross-walls or *septa*, depending on the kind of fungus. The hyphae increase in length at the tip (apical growth) and are commonly branched, often being interwoven so as to form a loose network,[1] or being organized into pseudo-tissue. There is no true tissue-formation in the fungi, for the cells do not have a common origin, as in the parenchyma of the higher plants.

All fungi are either saprophytes or parasites. In the case of saprophytes the decay of the substratum on which the fungus grows may be caused by the fungus itself, with or without the assistance of bacteria. Some fungi (*e.g.*, the Powdery Mildews and Rusts) live always parasitically, others (*e.g.*, the Meadow Mushroom and the Puffballs) live always saprophytically, while still others (*e.g.*, species of Molds, and the wood-destroying fungi) may grow either as saprophytes or parasites or, as in the case of the "damping-off" fungus that destroys young seedlings, may change from a parasitic to a saprophytic existence during the course of their development.

In contrast to most green plants, the fungi do not, so far as is known, elaborate starch but, instead, another carbohydrate, *glycogen*, which occurs more commonly in animals and is sometimes called "animal starch."

[1] The term hypha is from the Greek word, ὑφή (*hyphē*), meaning a web.

In some groups of fungi the hyphae, as noted above, are *septate*, *i.e.*, divided by cross-walls into cells; in other groups they are *aseptate* (without cross-walls), and have, therefore, only one mass of protoplasm. In such forms the protoplasm contains many nuclei distributed throughout its mass, forming a cellular complex called a *coenocyte*.[1] In certain fungi (*e.g.*, blue mold, *Penicillium*) the septa divide the filament into a series of smaller coenocytes.

Spore Formation.—The spores of fungi are either asexual or sexual. Asexual spores are formed in one of four ways:

1. By free abscission at the tip of a filament. Such spores are often called *conidiospores* or *conidia*[2] (Fig. 340). In some forms they are attached by a slender stalk or *sterigma*.

2. By the transformation of one of the cells of a filament, involving the formation about it of a thick cell-wall. Such a spore is a *chlamydospore*, so called from the Greek words, *chlamys* (mantle) and *spora* (seed).

3. By the transformation of the protoplasm of a cell into one or more motile spores (*zoöspores* or swarm-spores) which escape from the walls of the mother-cell, or into one or more non-motile spores which remain within the walls of the mother-cell. In the latter case the walls and cavity of the mother-cell constitute an *ascus* (sac), and the spores are *ascospores*. They may have from one to many cells (Fig. 339).

4. By the division of the multi-nucleate protoplasm of a sporecase into separate spores, as, for example, in the bread-mold (*Rhizopus*), as described in detail on pages 467–468.

Sexual spores, which occur in various groups of fungi, are formed (as always throughout the plant world) by the fusion of two cells. These cells may be morphologically similar (as, for example, in the molds), or they may be differentiated into egg-cells and sperm-cells, as, for example, in the powdery mildews (Fig. 339) and in the "damping off fungus." The diploid cells resulting from such fusion are variously called oöspores[3] or carpospores.[4]

[1] From two Greek words, *koinos* (κοινός), common + *kytos* (κύτος), hollow (container).

[2] From the Greek, *konis* (κόνις), dust.

[3] Oöspore, from the Greek, *oon* (ὠὸν), egg + *spora* (σπορά), seed. Called also an *oösperm* (*oon* + *sperma*, seed).

[4] Carpospore, from the Greek *karpos* (καρπός), fruit + *spora* (σπορά), seed.

Origin and Classification of Fungi.—The absence of chlorophyll, together with certain other characteristics, is evidence that the fungi are degenerate plants, derived from chlorophyll-bearing ancestors. In structure and modes of reproduction they resemble certain algae, and it is generally believed that they have been derived or evolved from various groups of the algae, and at various geological epochs. There is fossil evidence of fungi in rocks as old as the Devonian. Apparently the non-septate fungi were derived from non-septate algae, and septate fungi from septate algae.

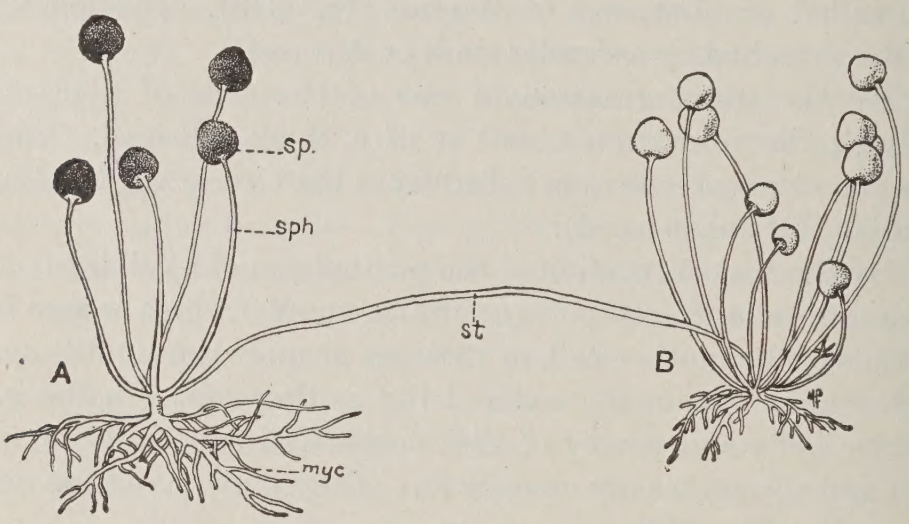


FIG. 329.—Bread mold (*Rhizopus nigricans*). *A*, older plant; *myc*, mycelium; *sph*, sporangiophore; *sp*, sporangium; *st*, stolon produced by *A*, and giving rise at its tip to a new plant, *B*. Greatly enlarged.

Fungi are classified in four major groups or Classes, as follows:

CLASSES OF FUNGI

MYCELIUM NON-SEPTATE:

1. *Phycomycetes*, alga-like fungi, so called because they closely resemble certain non-septate algae, except for lack of chlorophyll. There are two sub-classes, as follows:

   a. *Zygomycetes*, which reproduce sexually by the fusion (*conjugation*) of two similar gametes, *e.g*, the "Mucors" or Black Mold (*Rhizopus*), a saprophyte; and the "fly-fungus" (*Empusa muscae*), parasitic on flies.

   b. *Oömycetes*, which reproduce sexually by the union of an *oösphere* (egg) and a sperm to form an *oöspore* (oösperm).

e.g., *Phytophthora omnivora; Cystopus candidus* (the White Rust of radishes and other crucifers), and *Pythium debaryanum*, the so-called "damping-off fungus."

MYCELIUM SEPTATE:

2. *Ascomycetes*,[1] sac-fungi, having their asexual spores formed in sacs or *asci*. This class includes the Powdery Mildews, Morels, Yeast, and other forms.

3. *Basidiomycetes*,[1] with spores borne on little club-shaped hyphae or *basidia*. This group includes the Smuts, Rusts, and Mushrooms.

4. *Fungi-imperfecti*, called the "imperfect fungi" because their life histories are imperfectly known. As these life histories become completed the forms may be referred to one or another of the preceding classes. The fungus causing Early Blight of Potatoes (*Alternaria Solani*) and that causing Fruit Spot of Apples (*Cylindroosporium Pomi*) are among the large number of forms provisionally included in this group.

Number of Species of Fungi.—The number of species of fungi have been variously estimated at from 32,000 (Saccardo, in 1889, who included over 8000 *Fungi imperfecti*) to 150,000 (DeBary, in 1872). In an introductory course in general botany there is time to study only one or two forms in each of the large groups or classes.

An Alga-like Fungus (Rhizopus)

Habitat.—One of the most familiar of the Phycomycetes is the common Black Mold or "Bread Mold" (*Rhizopus nigricans*). This fungus will grow on almost any moist organic substance. The material on which it grows is called the *substratum*. To secure a culture it is only necessary to expose to the air a piece of moist (not wet) bread. The fungus will develop most readily on a cut surface (in preference to the crust). If the bread, as soon as cut from the loaf, is placed in a glass dish or pan and covered over with a glass bell-jar or plate the fungus will begin to appear within ten or twelve hours. This shows that spores of the fungus must have been present on the surface of the bread. When this fungus (wherever it may be growing) "fruits," its

[1] The Ascomycetes and Basidiomycetes, having a less simple structure than the Phycomycetes are, by some authors grouped as sub-classes under the Class, *Eu-mycetes* or True Fungi.

spores are discharged and widely disseminated by currents of air. They lodge on all surfaces, and are harbored in larger numbers by dust. Whenever dust is stirred up, the spores are again carried about in the air. Whenever objects are picked up, the spores of fungi (and also the various bacteria, yeast, and other "germs") may become transferred to the fingers and thence to the surface of any object subsequently handled. Thus, in preparing the bread as suggested above, some of the omnipresent spores are almost certain to be transferred to its surface, where they find conditions that favor germination. If one wishes to obtain a pure culture of a particular species of fungus it is, of course, necessary to sterilize the substratum so as to kill all spores and bacteria that may already be present, and then sow the spores of the species desired.

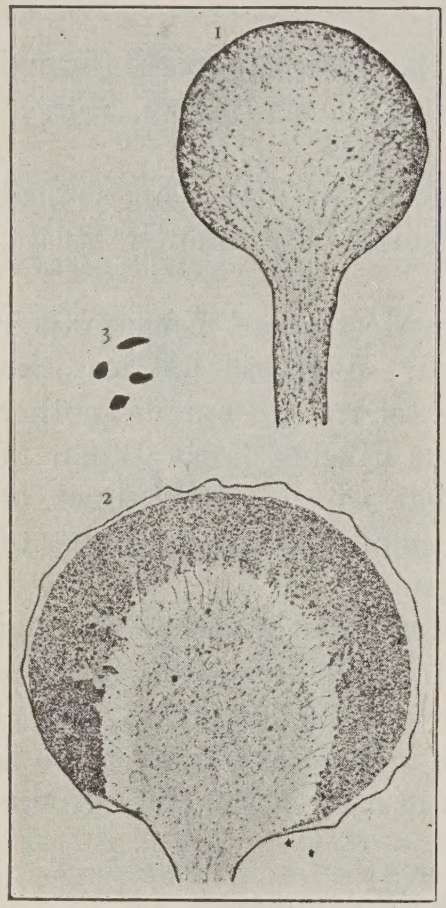


FIG. 330.—*Rhizopus nigricans*. 1, Young sporangium, showing cytoplasm and nuclei streaming up the sporangiophore into the sporangium and out toward the periphery. 2, Sporangium of nearly full size. The differentiation between the dense peripheral and the looser central plasms is clearly shown. Nuclei are still passing from the central to the peripheral regions along the fine strands of cytoplasm. × about 200. (After D. B. Swingle.) (Cf. Figs. 331 and 332.)

Partly as a result of the presence of the fungus the substratum on which it is growing begins at once to decay. The decay is merely the disintegration of the organic matter as a result of the action of enzymes secreted by the fungus, and often also by bacteria which may be present.[1]

Description of the Plant Body. The plant body of *Rhizopus* (Fig. 329) consists of a tangle of mycelial hyphae, branching freely, and growing over the surface and penetrating more or less into the substance of the substratum. Since the hyphae

[1] *Cf.* pp. 199–200.

are aseptate (without cross-walls), the plant body is a single coenocyte, with many nuclei distributed through the cytoplasm. When viewed under the microscope the hyphae are seen to taper toward the tip, and the protoplasm appears to be *streaming* in a constant current in one direction. There is some

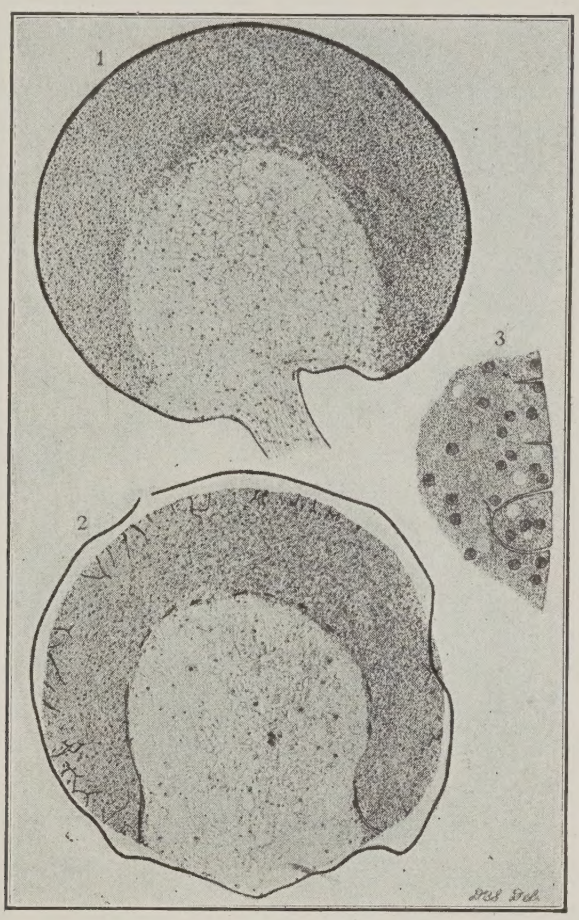


FIG. 331.—*Rhizopus nigricans.* 1, Full-sized sporangium, showing layer of vacuoles nearly formed along the inner surface of the denser plasm, × about 200. 2, Section passing to one side of the sporangiophore, showing columella-cleft being formed by fusion of the vacuoles shown in 1, and by a furrow from the base of the sporangium, × about 200; 3, Detail of another part of same sporangium as shown in 2, showing early cleavage furrows, × about 850. (After D. B. Swingle.) (Cf. Figs. 330 and 332.)

difference of opinion among investigators as to the cause of this streaming.

Secretion of a Powerful Poison.—In the course of some experiments, undertaken primarily for another purpose, Blakeslee and Gortner injected into the ear of a healthy rabbit some of the juice, squeezed out of the mycelium of *Rhizopus nigricans.*

To their great surprise the animal died almost instantly, before the injection was completed. Further experiments clearly demonstrated that *Rhizopus* contains a powerful poison (or *toxin*), which is soluble in water, but which produces its effect only when introduced into the circulatory system. When this expressed

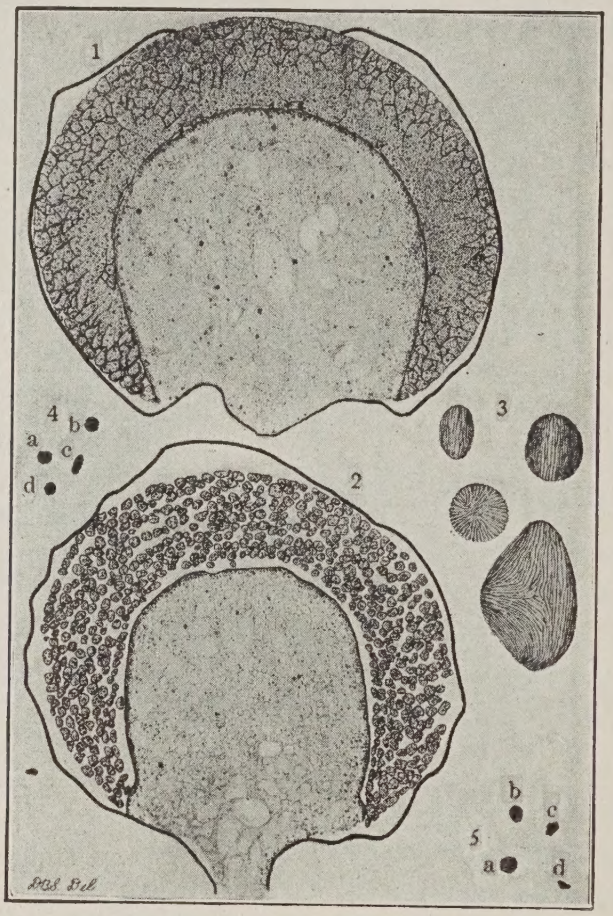


FIG. 332.—*Rhizopus nigricans*. 1, Section of sporangium, showing cleavage of peripheral cytoplasm much further advanced than in Fig. 331. Furrows are here cutting outward from the columella cleft, × about 200; 2, section of sporangium in which the spores are completely formed, rounded up, and surrounded by thin walls. The columella wall is also formed, × about 200; 3, ripe spores in their living condition, showing variations in size, and ridges on their walls, × over 350. (After D. B. Swingle.) (Cf. Figs. 330 and 331.)

juice was fed to the rabbits, or when they ate the mycelium, no harmful result followed.

Vegetative Multiplication.—At various points the mycelium produces one or more upright, aerial hyphae, 15 to 20 millimeters high, and of larger diameter than the mycelial hyphae. One or more of these hyphae eventually bend over and grow for a

short time along the surface of the substratum, like the stolons or "runners" of such plants as strawberries. Finally, at their free ends there develop slender hyphae that penetrate the substratum, like rhizoids, and another group of the larger, aerial hyphae, one or more of which may repeat the process just described. The formation of these stolons suggested a former name of the plant, viz., *Mucor stolonifer*.

Asexual Reproduction.—At the tip of each upright hypha there develops a globular sporangium, and hence the hypha is called a *sporangiophore* (Fig. 329). The protoplasm, containing a large number of nuclei, is constantly streaming up the sporangiophore, getting more and more dense toward the sporangium. Further down, toward the base of the sporangiophore, the pro-

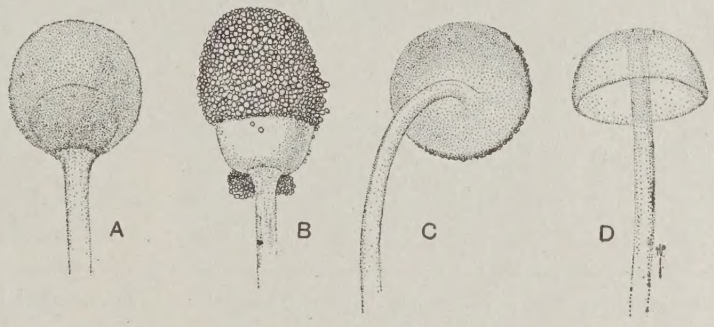


FIG. 333.—*Rhizopus nigricans*. *A*, Young sporangium, showing columella within; *B*, older sporangium, with the wall removed, showing ripe spores covering the columella; *C*, *D*, views of the collapsed columella after dissemination of the spores.

toplasm becomes thinner and thinner, and the nuclei, fewer in number, finally disintegrate. In the meantime the tip of the sporangiophore increases in size until the globular sporangium is formed, rich in cytoplasm and nuclei. By degrees the protoplasm becomes more dense toward the periphery, and gradually thinner toward the central portion, where large numbers of vacuoles develop. Soon a well-marked cleft separates the denser peripheral protoplasm from the thinner central portion, which now develops into a little column, or *columella* (Fig. 331). The cleft is formed by the flattening and fusing of the vacuoles and by the cutting upward of a circular furrow from the base of the sporangium to meet the cleft formed by the vacuoles. In the meantime innumerable furrows develop in the denser plasm, first at the periphery and then working their way in from the columella cleft. By the time the two sets of furrows meet, the

dense protoplasm has been cut up into innumerable, more or less angular masses, each surrounded by a plasma-membrane, and containing from two to six nuclei each (Fig. 332). These masses finally become entirely separated from each other, oval in shape, and surrounded by a cellulose wall, having clearly marked ridges (Fig. 332). They are asexual spores, but differ from the spores of ferns, mosses, liverworts, and algae by usually, if not always, possessing more than one nucleus. They secrete a slimy substance in which they are imbedded. When ripe the wall of the sporangium bursts open (Fig. 333), and the spores, thus set free, float away through the air in countless millions.

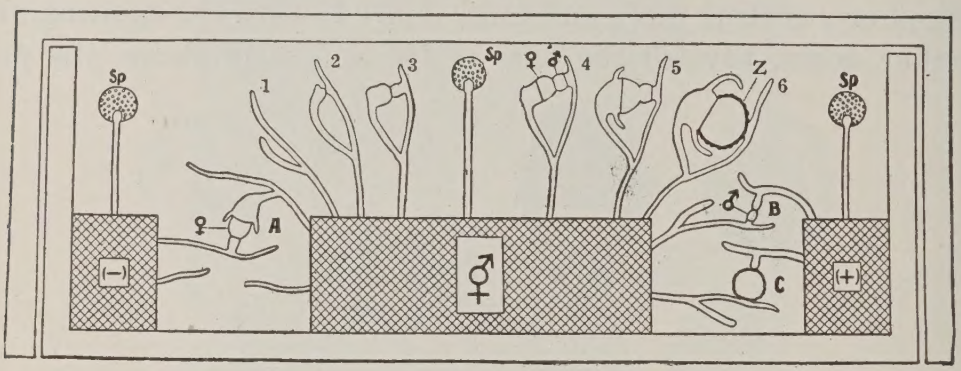


FIG. 334.—Sexual reaction between a hermaphroditic *Mucor* and (+) and (−) races of a dioecious species. Diagrammatic representation of a Petri dish culture showing a heterogamic hermaphroditic mucor $\left(\frac{\sigma}{+}\right)$ in the center separated by channels on either side from the (+) and (−) races, respectively, of a dioecious species. *Sp.*, sporangia containing spores by means of which the plant may be reproduced nonsexually. 1–6, stages in development of a hermaphroditic zygospore from unequal male and female gametes. *A*, sexual reaction between a (−) filament and female gamete. *B*, sexual reaction between a (+) filament and male gamete. *C*, a male zygospore formed by stimulus of contact with a (+) filament. (After Blakeslee.)

So widely and so thickly are they distributed that a piece of moist bread, or a jar of canned fruit, left exposed for only a brief period, in almost any locality, will, as noted above, soon become "moldy" from the growth of mycelium produced by their germination. On account of the practically universal distribution of "bread mold" its spores are, of course, commonly present in the air of laboratories, where the mold is a great pest, and has therefore won the appropriate title of "laboratory weed."

Sexual Reproduction.—When the hyphae of mycelia derived from spores of different sex-value are intermingled they frequently develop short lateral branches, which grow out toward

each other until their tips come in contact (Fig. 334). The rich protoplasmic contents at the tips are cut off from the remainder of the coenocytic mycelium, the walls in contact with each other become dissolved,[1] and the two protoplasmic masses fuse. This will be recognized as conjugation; the fusing masses of protoplasm are *isogametes*, and the cut-off tips of the conjugating branches function as *gametangia*. After the *zygote* is

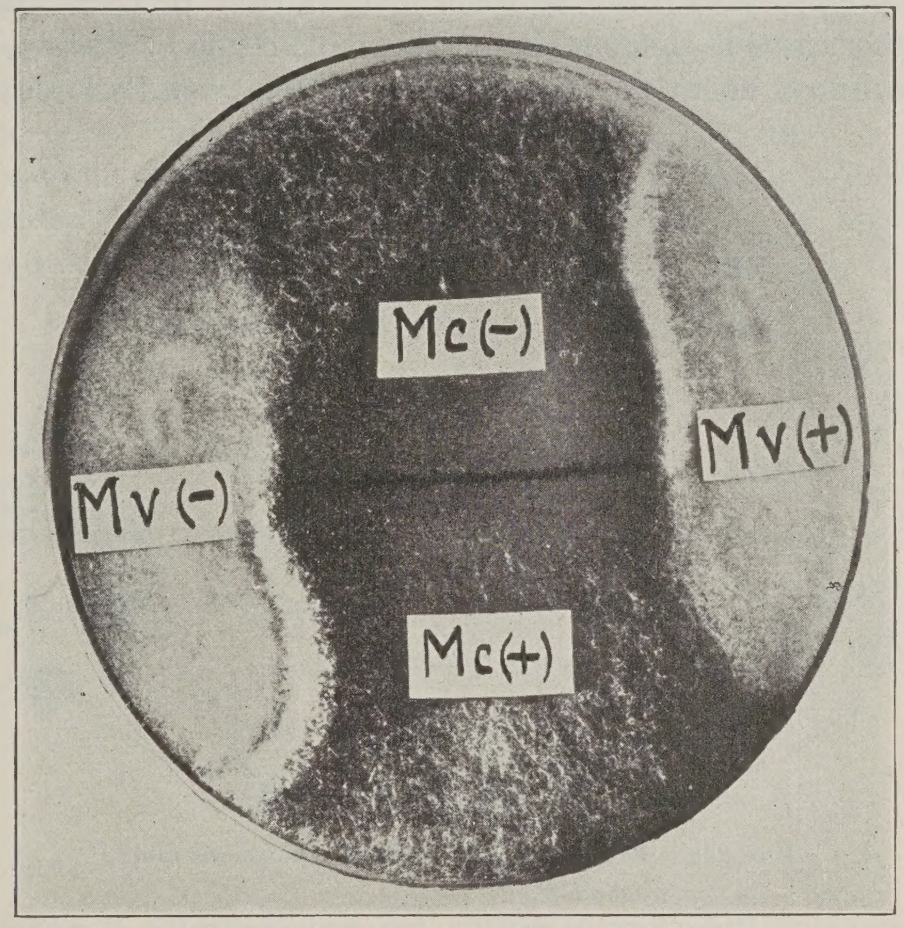


FIG. 335.—Petri-dish culture showing dark line of zygospores between the (+) and (−) strains of a dioecious species of mold, *Choanephora* (Mc) and white lines of "imperfect hybridization" between the strains of this species and the opposite strains of Mucor V (Mv). Note the total absence of zygospore formation between two (+) or two (−) strains. (After Blakeslee.)

formed, the outer wall thickens and assumes certain external characteristics, easily recognized. It also becomes black as it ripens, and this fact, together with the black color of the ripe sporangia, has given rise to the common name, "black mold." In this condition the *zygote rests*, as a *zygospore*.

[1] Probably by enzyme action, though this has not been actually demonstrated.

Germination.—At the close of the resting period, and under favorable conditions of temperature and moisture, the zygote germinates, sending out an erect hypha, which at once develops a globular sporangium at its apex. The asexual spores from this sporangium become the starting point of another series of changes like those just described.

Sexuality of Rhizopus.—It is well known that, while conjugation often occurs freely between mycelia from different spores, in other cases it fails entirely. The explanation of this was not known until about twenty years ago (1904), when Blakeslee dis-

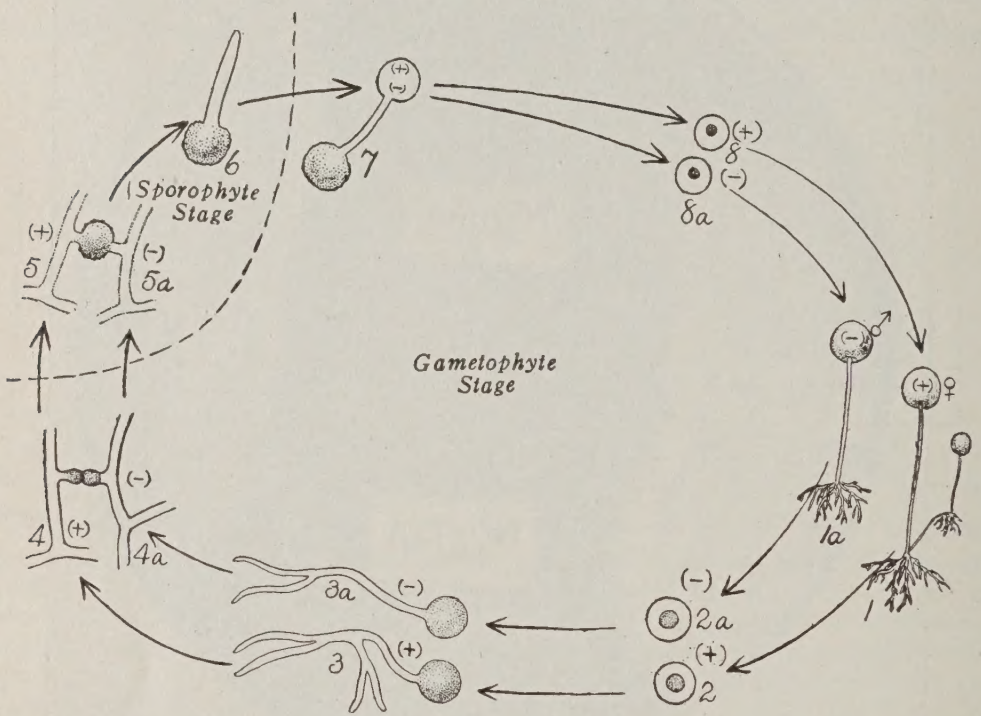


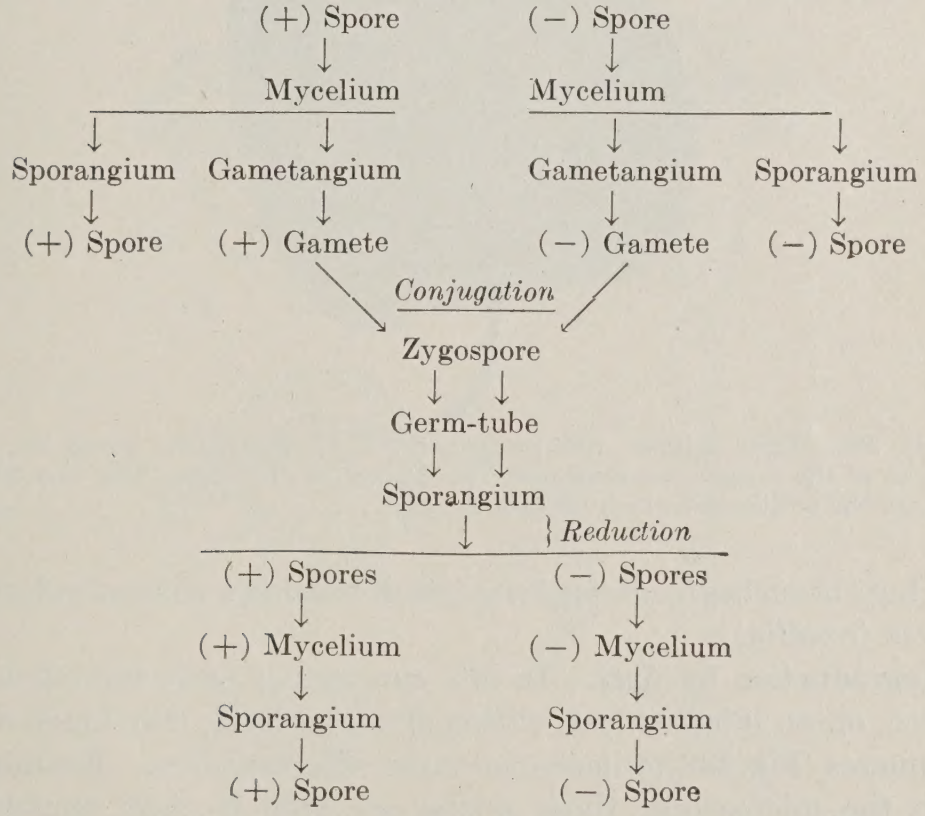
FIG. 336.—Diagram of life-cycle of a dioecious mold.

covered that there are, in reality, two unlike strains of *Rhizopus*-mycelium, and therefore two kinds of spores. The two kinds of mycelia are designated as (+) and (−). When the intermingling hyphae are of like strains, either all (+) or all (−), they are *homothallic*, and conjugation fails completely; but when they are from strains that are unlike (*heterothallic*), zygospores form in great abundance. This fact is strikingly shown in Fig. 335, which illustrates the result of growing mycelia from unlike strains side by side. The zone where they come into contact is sharply defined by the line of black zygospores, resulting from conjugation.

Distinction of Sexes.—When first discovered, the two unlike strains were designated as (+) and (−), because it was not possible to decide, with certainty, which was male and which female. Externally both strains looked very much alike, except that one appeared to be vegetatively more vigorous than the other. Experiments seem to indicate that the vegetatively more vigorous (+) strain is female, while the less vigorous strain is male.[1] Not all molds are *dioecious*, like *Rhizopus*. In some species the mycelium from a single spore produces conjugating branches of both (+) and (−) value, which fuse and form a zygospore. Such mycelia are, of course, monoecious.

Life-cycle of Rhizopus.—The life-cycle of a dioecious mold is illustrated in fig. 336. The life-history of *Rhizopus* may be diagrammed as follows:

Outline of Life History of Rhizopus



[1] Recent experiments of Satina and Blakeslee show that, on the average, the races of a (+) sex have a greater power to reduce the salts of tellurium (*e.g.*, Na_2TeO_3) than have those of the (−) sex. (*Satina, Sophia & A. F. Blakeslee.* Studies on biochemical differences between (+) and (−) sexes in mucors. Proc. Nat. Acad. Sci. **11**: 528-534. Sept., 1925. Genetics **11**: 528. 1925.)

Sac Fungi

a. **Powdery Mildew** (*Microsphaera*).

Habitat and Structure.—The fungus, *Microsphaera*, may be found growing on the leaves of the lilac, honeysuckle (*Lonicera*), birch, oak, hickory, walnut, and other plants, and is commonly called "powdery mildew." The mycelium is *septate*, and forms a web over the surface of the leaf (Fig. 337), sending down *haustoria* into the epidermal cells, to secure nourishment, and sending

FIG. 337.—Lilac mildew (*Microsphaera Alni*). The white areas are the mycelia of the fungus, growing over the surface of the leaf. The tiny black dots are the perithecia, which contain the asci.

up short branches (*conidiophores*), each bearing a chain of colorless spores (*conidia*).

Reproduction by Asci.—In late summer or early fall one may notice, on an infected leaf, within the mycelium, tiny black dots or spheres (Fig. 338), whence the name, *Microsphaera*. Examined with the microscope, these bodies are seen to bear numerous appendages, branched at the end, and with the tips of the branches curved back to form miniature hooks (Fig. 339). When these little spheres are crushed, or when they burst open, they are found to contain a number of tiny sacs or *asci* (singular, *ascus*),

FIG. 338.—Powdery mildew (*Microsphaera Alni*) on lilac leaf. An infected area from the leaf in figure 337, greatly magnified.

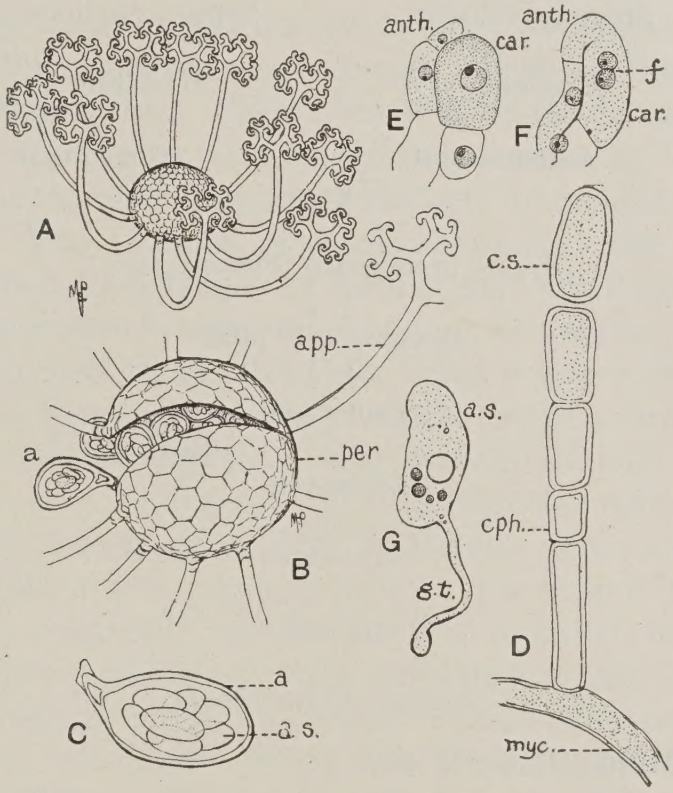


FIG. 339.—Lilac mildew (*Microsphaera Alni*). *A*, perithecium, with appendages; *B*, perithecium, showing asci (a); *C*, an ascus, containing ascospores; *D*, conidiophore (*cph*), bearing a chain of conidia (conidiospores, *c.s*); *E*, beginning of fertilization; *anth*, antheridium; *car*, carpogonium; *F*, later stage in fertilization; the contents of the antheridium and carpogonium have fused; *f*, fusion of the two nuclei; *G*, germination of ascospore (*a.s*); *g.t*, germ tube. (*E* and *F* after R. A. Harper.)

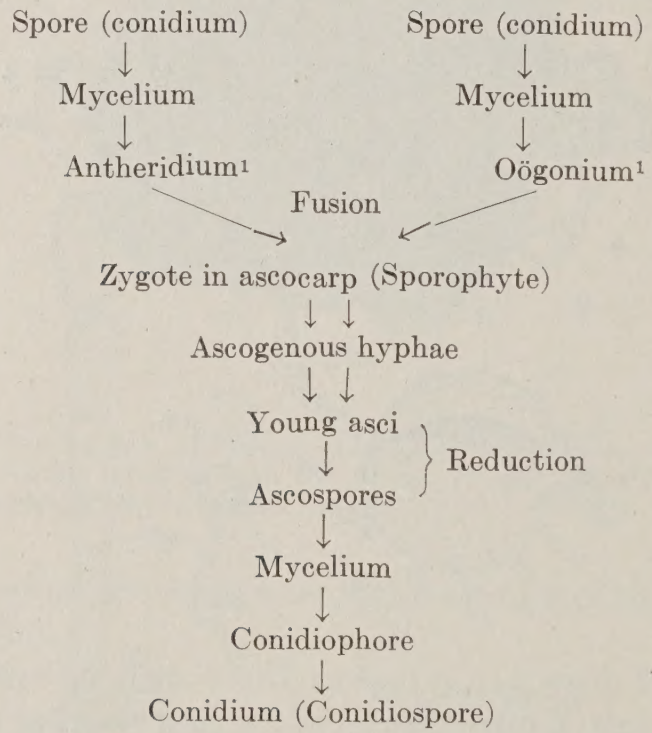
whence the name "sac-fungus," or *Ascomycete*. In each ascus are a number of *ascospores*, formed from the contents of the ascus. The young ascus, is, therefore, a spore-mother-cell. There are usually eight ascospores in an ascus, but the number may vary from 2 to 8, according to the species.

The spherical case containing the asci is the "spore-fruit" (*ascocarp* or *perithecium*), and results from the fusion of the contents of an antheridium and an oögonium (Fig. 339). The cells from this point on, to the formation of the ascus, are diploid, and therefore constitute the sporophytic generation.

Germination.—When an ascospore germinates it develops directly a hypha.

Life-cycle.—The life-cycle of *Microsphaera* may be diagrammed as follows:

Outline of Life History of Microsphaera



b. **Blue Mold** (*Penicillium*).

Habitat and Structure.—The various species of *Penicillium* are able to grow on a great variety of substrata, and are therefore widely distributed—even more so than *Rhizopus*. Like the

[1] In *Microsphaera* there is only a slight morphological differentiation of the gametes.

mucors, the plant body consists of a network of mycelium forming a mat on the surface of the substratum. Some of the hyphae penetrate the substratum. In contrast to *Rhizopus* the hyphae of *Penicillium* do not taper toward the end but are cylindrical to the tip.

The hyphae are septate, and the protoplasm between the cross-walls occurs as a lining pressed against the wall, with various strands extending from one side to the other across the large central vacuole. There are several nuclei (usually 4–8) in each compartment which is, therefore, a coenocyte. In contrast to *Rhizopus*, the terminal coenocyte is rounded or convex at the tip and more completely fills the cell-cavity, having numerous small vacuoles instead of one large central vacuole. Growth is largely, if not wholly, confined to the terminal cell. *Penicillium* is capable of living without access of free oxygen (anaerobically). Under such circumstances it acts as a ferment (like yeast), converting the substratum into carbon dioxide and alcohol.

Asexual Reproduction.—At certain places on the mycelium upright branches arise. These become divided by cross-walls into four or five coenocytes, and finally they branch at the tip, in a characteristic manner, forming a delicate branch-like structure (Fig. 340). The terminal branches taper to a fine point, the *sterigma*, which soon bulges to form a tiny, spherical, one-celled spore. This process is repeated over and over again until a chain of spores is formed, those at the base being younger than those at the tip. The spores are *conidia*, and the fruiting structure that bears them is a *conidiophore*. The conidia are only about two thousandths of a millimeter (2μ) in diameter and are easily blown away, becoming widely scattered. The walls of the conidia contain a blue pigment, whence the name "blue-mold." They occur commonly in the air we breathe, indoors and out. When the conidia fall on a moist surface they may germinate, producing a hypha and finally a mat of mycelium, thus completing a life-cycle. When the conidia germinate under anaerobic conditions they form buds, behaving like the cells of the yeast plant.

Sexual Reproduction.—When *Penicillium* grows anaerobically, or with a very small proportion of oxygen in the surrounding air, it reproduces as follows: Short cylindrical branches develop

close together in pairs at intervals on the hyphae, and coil about each other forming a spiral. These branches are called *gametangia*, and it is believed that their protoplasmic masses fuse, but the process has never been actually observed. After the coiling of the gametangia they give rise to numerous short

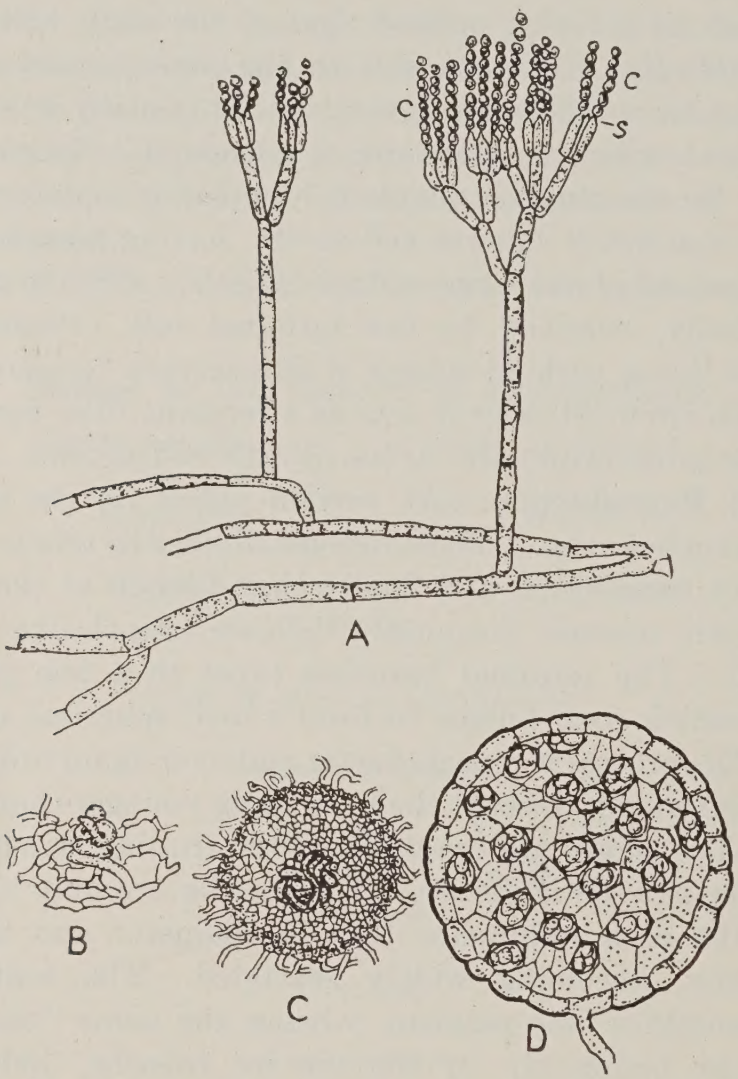


FIG. 340.—*Penicillium glaucum*, × 400. *A*, part of the mycelium with conidiophores. *s*, sterigma; *c*, spores (*conidia*). *B*,*C*, and *D*, stages in the formation of the ascocarp. (From Dixon after Brefeld.)

branches (*ascogenous hyphae*), and at the same time the main hyphae near the gametangia produce numerous branches which finally surround and cover the gametangia with an intricate, spherical network of several layers. A yellow pigment develops in the cell-walls of the outer layers, which also become hard and

form a tough membrane or skin protecting the parts within. This whole structure is the *ascocarp* (Fig. 340). After a short interval the ascogenous hyphae produce hooked branches which bear chains of egg-shaped cells. These are the spore-sacs or *asci*, and within each ascus there develop eight *ascospores*, each about twice the size of a conidium. Haustoria-like branches also develop from the ascogenous hyphae, absorb all the material within the wall of the ascocarp, and deliver it as nourishment to the growing ascospores. The walls of the asci become liquefied (doubtless by enzyme action), and thus the ascospores come to lie free within the wall of the ascocarp. This entire process may require from six to eight months. When the ascocarp dries, the wall splits open and, under favoring conditions, the ascospores germinate, forming mycelium and thus initiating another life cycle.

Economic Importance.—Not only are the spores of *Penicillium* widely distributed, but the mycelium secretes an unusually large number of enzymes, so that the plant is able to digest (*i.e.*, liquefy) a great variety of substances which it can utilize for food. Few, if any, plants, are known that produce such a variety of enzymes. It secretes cytase which dissolves cell-walls (cellulose), diastase which changes starch to sugar, lipase which liquefies fats, protease for digesting certain proteins, catalase which liberates oxygen, and others.

It is to *Penicillium* that we are indebted for the flavor of some of our most highly prized varieties of cheese. The ripening of cheese is brought about by the action of bacteria on the curd, but other factors enter into the flavor. The green color and the flavor of Roquefort cheese (made from sheep's milk) are caused, at least in part, by the presence of a green form, *Penicillium roqueforti* Thom. The same species is the characteristic fungus in Gorgonzola and Stilton cheese. *Penicillium camemberti* (and also another fungus, *Oidium lactis*), growing on the surface of Camembert cheese, secretes an enzyme which penetrates into the body of the cheese, and thoroughly digests the protein of the curd. A number of species of bacteria and molds are involved in the ripening and flavor of this cheese. *Penicillium roqueforti* is also commonly found in ensilage, but its rôle here, if any, is not well understood.

Other Sac-fungi.—Between 25,000 and 30,000 species of sac-fungi have been described. Some of them are filamentous, like the lilac-mildew, while some are fleshy, like the common "cup-

FIG. 341.—A "cup-fungus," *Peziza sylvestris*. (Photo by F. J. Seaver.)

fungi" (Fig. 341). The edible morel, *Morchella esculenta* (Fig. 342) is an Ascomycete, and the common yeast, referred to in the chapter on fermentation (Fig. 92), is also classed here

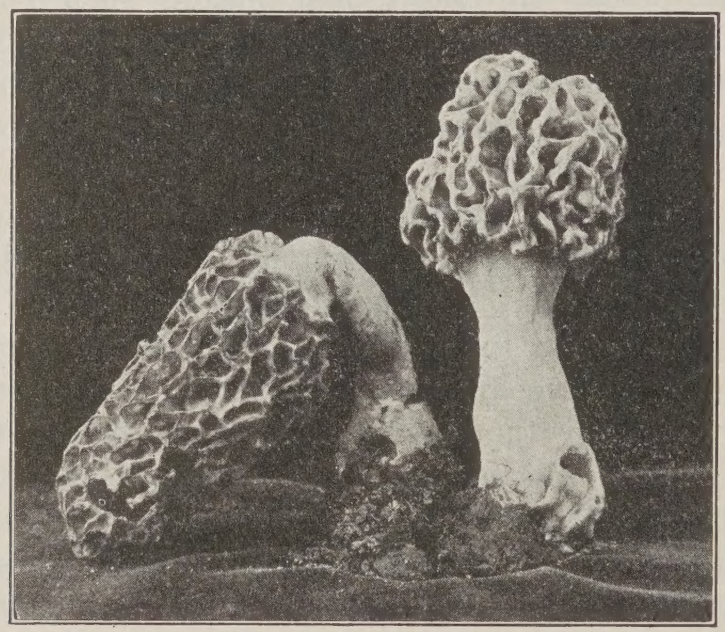


FIG. 342.—The morel, *Morchella esculenta*. (Photo by W. A. Murrill.)

because, in one of its methods of reproduction, the unicellular plant-body functions as a spore-mother-cell, the protoplast becoming organized into spores (ascospores), and the wall of the mother-cell serving as an ascus.

CHAPTER XXIII

CHARACTER AND LIFE HISTORIES OF FUNGI (CONCLUDED)

BASIDIOMYCETES

Classification.—The Basidiomycetes have been briefly characterized on a preceding page as fungi that bear their spores on basidia, whence the name of the group. Not all of the forms, however, have the characteristic basidia that occur in the toadstools and other fleshy members of the Class, and the various species, numbering about 14,000, readily fall into one of two Series, each of which, in turn, comprises two subdivisions. In the simpler groups the basidium is represented by a structure called the *promycelium*, to be described in the following paragraphs. Stated in tabular form, the four groups are as follows:

BASIDIOMYCETES

Series I. *Protobasidiomycetes* (*Hemibasidiomycetes*), simpler forms having promycelia.

1. The rusts (*Uredinales*)
2. The smuts (*Ustilaginales*)

Series II. *Eubasidiomycetes*, having true or typical basidia.

3. *Hymenomycetes:* Spores borne on a fruiting surface (*hymenium*)
   a. *Agaricaceae:* Hymenium borne on *gills.*
   b. *Polyporaceae:* Hymenium in many tubes or *pores.*
   c. *Hydnaceae:* Hymenium on "*teeth.*"
   d. *Thelephoraceae;* e. *Clavariaceae;* f. *Tremellineae.*
4. *Gasteromycetes:* The basidia line the inner walls of pouches or *cavities* in the fruiting body, which are closed until the spores are mature. The puff-balls, earth-stars, carrion-fungi, and nest-fungi belong here.

Series I. Protobasidiomycetes

A RUST FUNGUS (STEM RUST OF WHEAT)

Uredinales

Importance.—One of the most important, as well as most difficult, fungi to understand is the stem rust of wheat (*Puccinia graminis*). This fungus is important because it attacks some of the most valuable of all agricultural crops (wheat, oats, rye, barley, etc.) causing, at times, millions of dollars worth of damage.[1] It is difficult to understand because it is *heteroecious*—that is, lives alternately on two different plants, the barberry and the grain. This is called *heteroecism*. For many years the form on the grain was supposed to be quite another plant from that on the barberry, which was called *Aecidium berberidis*. With the exception of *Sclerotinia ledi*, belonging to another order of fungi (*Pezizales*), the rusts are the only fungi that are heteroecious.

Life History. *a. Red Rust Stage.*—The mycelium of red rust (*uredo stage*) grows between the cells of the stem and leaves of the wheat, or other grain, and finally during the summer, numerous sporophores, bearing one celled (but binucleate) red spores (*urediniospores*), break through the epidermis (Figs. 343, *B* and 344, *a–e*), producing reddish or rusty-looking dots and lines (the *uredinia*), whence the name "rust" for the plant.[2] The number of one-celled urediniospores produced on a single wheat plant a mounts to many millions; the number on all the infested plants of a wheat field is quite beyond comprehension. From a single spore several thousand new spores may be produced in seven or eight days in favorable weather, and several such generations may follow each other in the course of a few weeks. They are easily blown about by the wind to other wheat plants where they germinate and thus spread the rust widely and rapidly.

[1] The loss from stem-rust of wheat in the United States amounted to an average of over 30 million bushels for the years 1919–1923. The average farm price for these five years was slightly over $1.28 per bushel, making the average annual loss over $38,400,000.

[2] Before the life cycle of the rusts was understood, the red rust stage on wheat was regarded as a genus, *Uredo*, distinct from, and not related to *Puccinia*. This is the origin of the terms *uredinia* and *urediniospore* (also called *uredospore*). *Uredo* is a Latin word meaning *blight*.

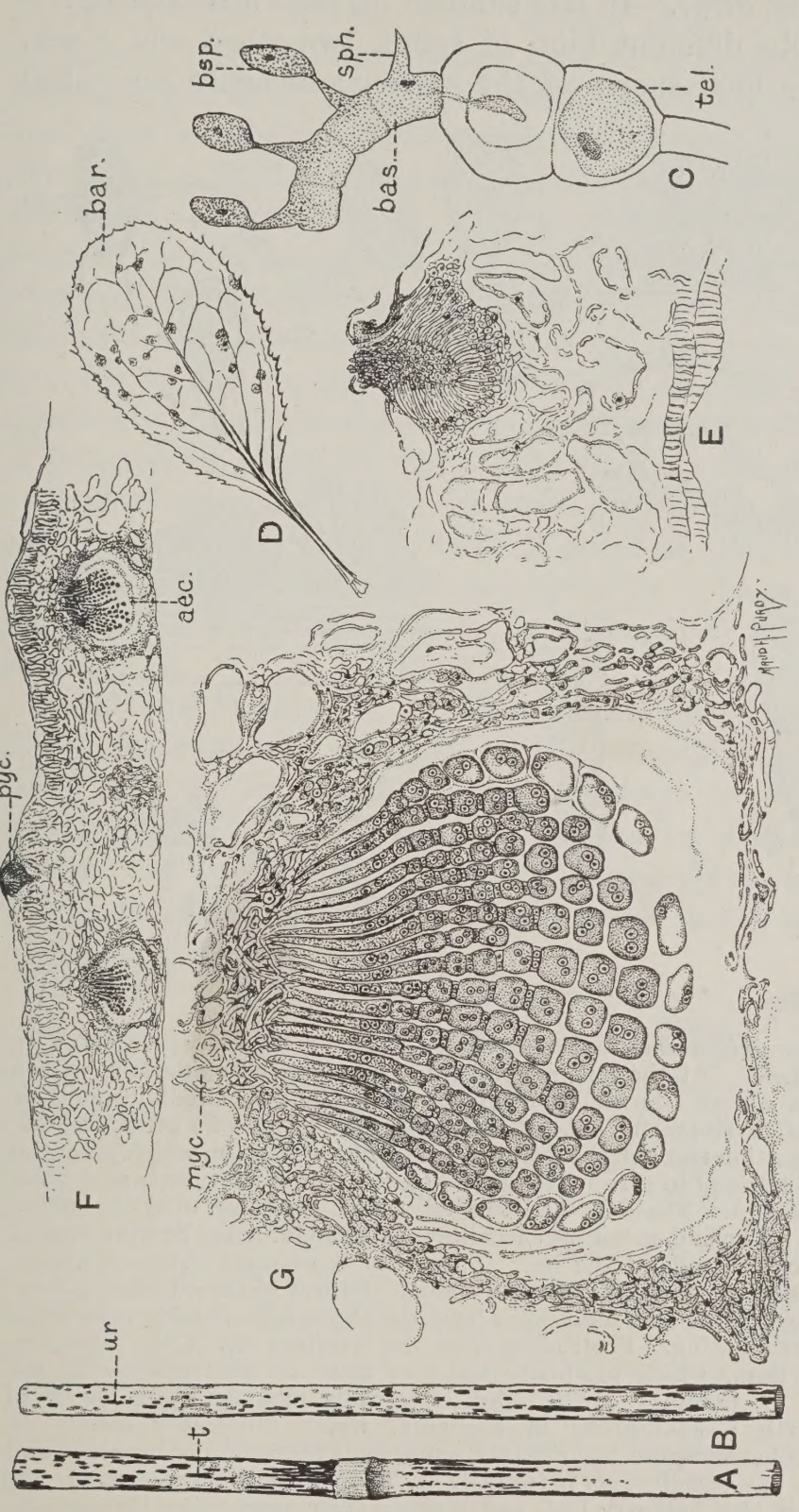


FIG. 343.—Wheat rust (*Puccinia graminis*). *A*, black rust stage on stem of wheat; *t*, sorus of teliospores; *B*, red rust stage; *ur*, sorus of urediniospores; *C*, teliospore germinating; *bas*, basidium; *sph*, sporophore (sterigma); *bsp*, basidispore (sporidium); *D*, leaf of barberry, showing numerous "cluster-cups" (aecia), bearing aeciospores; *E*, longitudinal section through a pycnium (spermagonium), formed at the upper surface of the barberry leaf; *F*, cross-section of a barberry leaf, showing a pycnium (above) and two aecia (*aec*); G, longitudinal section of an aecium, greatly enlarged, showing the mycelium of the fungus (*myc*), and the aeciospores, each with two nuclei. The walls of the cluster-cup are formed by the mycelium of the fungus. *C*, from *Puccinia Lygodesmiae*. (*C*, *E*, *F*, and *G*, from preparations of E. W. Olive.)

b. Black Rust Stage.—In late summer *the same mycelium* develops an entirely different kind of spore, two-celled and black. These are the final spores of the season and hence are called

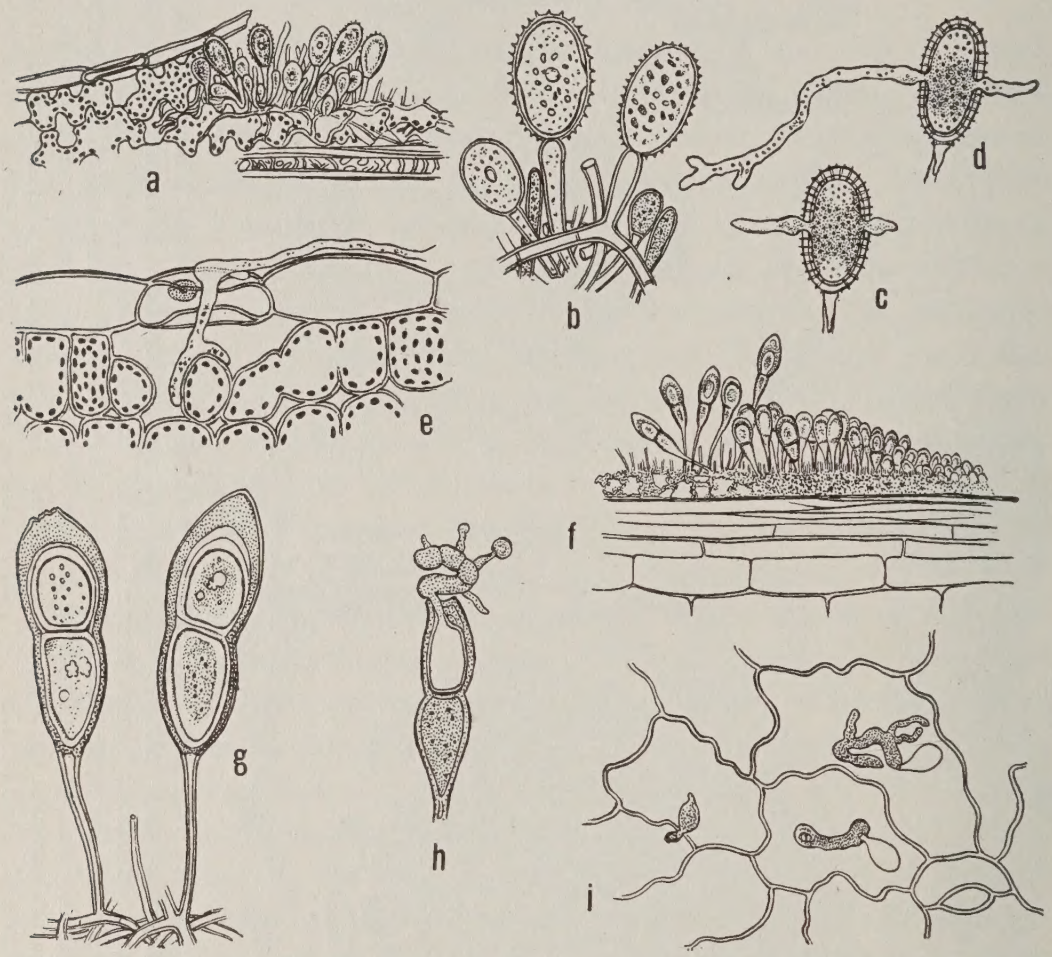


FIG. 344.—*Puccinia graminis.* *a*, Section through a urediniospore sorus on green leaf of wheat. At the left, a portion of the ruptured epidermis, with a guard-cell of a stoma shown in longitudinal section; *b*, Urediniospores in various stages of development; *c-d*, stages in the germination of a urediniospore; *e*, Longitudinal section through the leaf of a young wheat plant on which urediniospores had been allowed to germinate for 48 hours. The germ tube is seen passing through a stoma. The tube had formed a slight swelling over the stoma before entering. The end of the tube has branched, the branches passing around one of the mesophyll cells of the leaf; *f*, group of teliospores obtained from a longitudinal section of a dry, ripe straw of wheat. Some sori show both urediniospores and teliospores; *g*, Two teliospores from the above sorus, highly magnified; *h*, Teliospore germinating. Protruding from the terminal cell of the teliospore is the promycelium, which gradually acquires most of the contents of the teliospore-cell. It becomes divided by cross-walls into 3–5 cells, each of which puts forth a sporophore or sterigma, which ultimately forms, at its tip, a minute basidiospore (sporidium); sometimes the sterigma branches and then more than one basidiospore is formed. *i*, Three basidiospores germinating on the epidermis of a barberry leaf, and sending their germ-tubes through the cuticle into the tissue of the leaf. Eventually this mycelium produces the aecia on the barberry leaf. Cf. Figs. 343 and 345. (Redrawn from Marshall Ward.)

teliospores (teleutospores) (Figs. 343 and 344). As explained in paragraph *c* below, each of the cells of the young teliospores possesses *paired nuclei*, but as the spores mature these nuclei fuse, thus completing the "fertilization" process begun with the cell-fusion in the formation of the aeciospore. In this condition the spores rest over winter. In fact a period of rest appears to be necessary for the teliospores, and may be considerably prolonged. Marshall Ward found that teliospores kept in his laboratory for as long as three years would still germinate. They normally germinate the following spring, each cell usually sending forth a hypha commonly composed of four cells; this constitutes the *basidium* or *promycelium* (Figs. 343 and 344). Each of these cells produces a tiny *sporophore*, bearing at its tip a single uninucleate *basidiospore* (*sporidium*). During the cell divisions that take place in the germination of the teliospore a reduction of the chromosomes takes place, and the gametophytic (haploid) stage is again initiated.

c. Barberry Stage.—The basidiospores are blown by the wind to the leaves of nearby barberry bushes. Certain species of barberry (*e.g.*, the Japanese barberry) appear to be immune to the rust, but when the basidiospores fall on the leaves of a susceptible species they germinate. The resulting mycelium penetrates the epidermis and ramifies between the cells of the leaf-parenchyma, from which it absorbs nourishment.

Near the *lower* epidermis are formed the "cluster cups" or *aecia* (sing., *aecium*), formerly called *aecidia*. They break through to the outer surface and contain countless hyphae which have undergone cell-division at the tip (Fig. 346). At a certain stage of development numerous cells are formed, rich in protoplasm and having nuclei larger than those of the adjacent cells. After a resting period this cell is entered by a nucleus from an adjacent cell, which passes by an amoeboid movement through the cell-walls. The nuclei do not fuse but, from this point on, the condition of *paired nuclei* continues—in the aeciospores, in the mycelium that bears urediniospores, and in the young teliospores. This corresponds to the sporophytic stage in the alternation of generations in higher plants. Fusion of the nuclei takes place during the maturing of the teliospore and then the uninucleate condition continues until the aecia are again formed.

Blackman,[1] describing this process for *Phragmidium violaceum* (another species of Uredineae), says that "such a series of phenomena leave no escape from the view that the fertile cell is a female reproductive cell which undergoes a process of fertilization," except that the fertilization is accomplished by an undifferentiated vegetative cell and not by a specialized cell or sperm. After the cell-fusion the fertile cell divides several times rapidly (the nuclei dividing separately and not fusing), thus forming a number

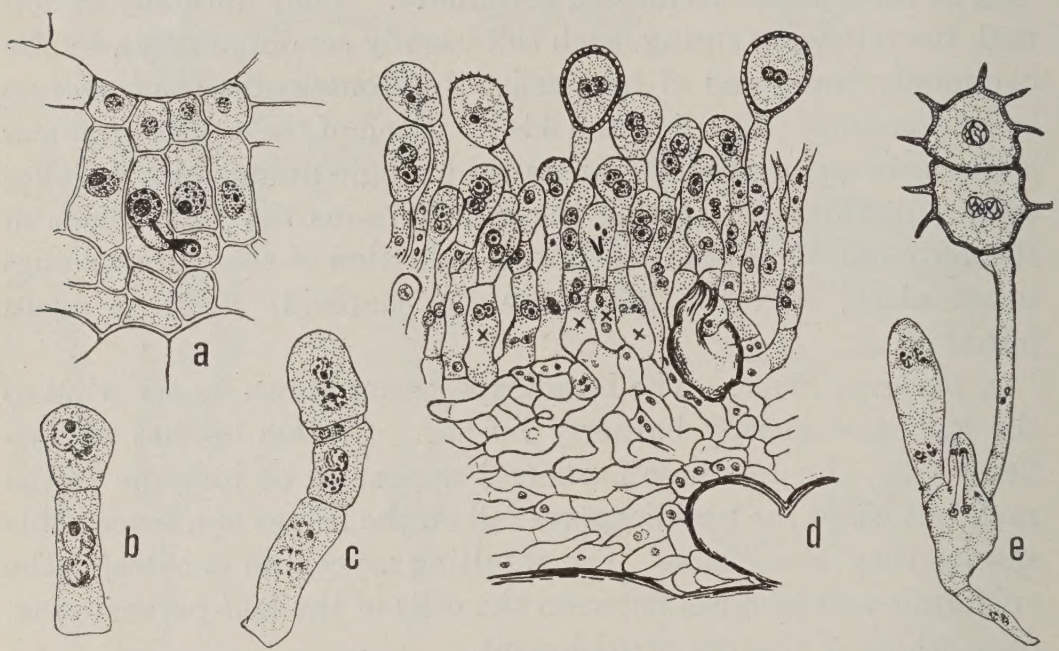


FIG. 345.—*a-d, Phragmidium violaceum. a,* portion of a young aecium showing the nucleus of the basal cell, below one fertile cell, migrating through the cell-wall into an adjacent fertile cell; *b,* fertile cell which has cut off the first aeciospore-mother-cell; *c,* cell-row of aecium showing (from above downwards) young aeciospore, intercalary cell, aeciospore-mother-cell, and fertile cell; *d,* Group of developing urediniospores on perennial mycelium (from stem of *Rubus*), with four basal cells marked *x*.

e, Teliospores of *Puccinia podophylli* in various stages of formation. Note that the cells of the mycelium each contain two nuclei. Semi-diagrammatic. (*a-d,* redrawn from V. H. Blackman; *e,* redrawn from A. H. Christman.)

of *aeciospore-mother-cells,* which in turn give rise by cell-divisions to the *binucleate* aeciospores (Fig. 345).

Buller[2] calculated that a single aecium examined by him contained about 11,000 spores. There are from three or four to 150 aecia in a single leaf-pustule, and there may be 18–20 or more

[1] Blackman, Vernon H. On the fertilization, alternation of generations, and general cytology of the Uredineae. Ann. Bot. **18**: 323–370. 1904.

[2] Buller, A. H. Reginald. Researches on fungi. **3**: 550. 1924.

pustules on a single leaf. Buller calculated further that one leaf may produce as many as 4,000,000–8,000,000 aeciospores, and a single bush of 200 leaves as many as 100 million spores. When ripe, the aeciospores do not merely fall out, but are violently discharged or shot away into the air, and carried off by the wind.

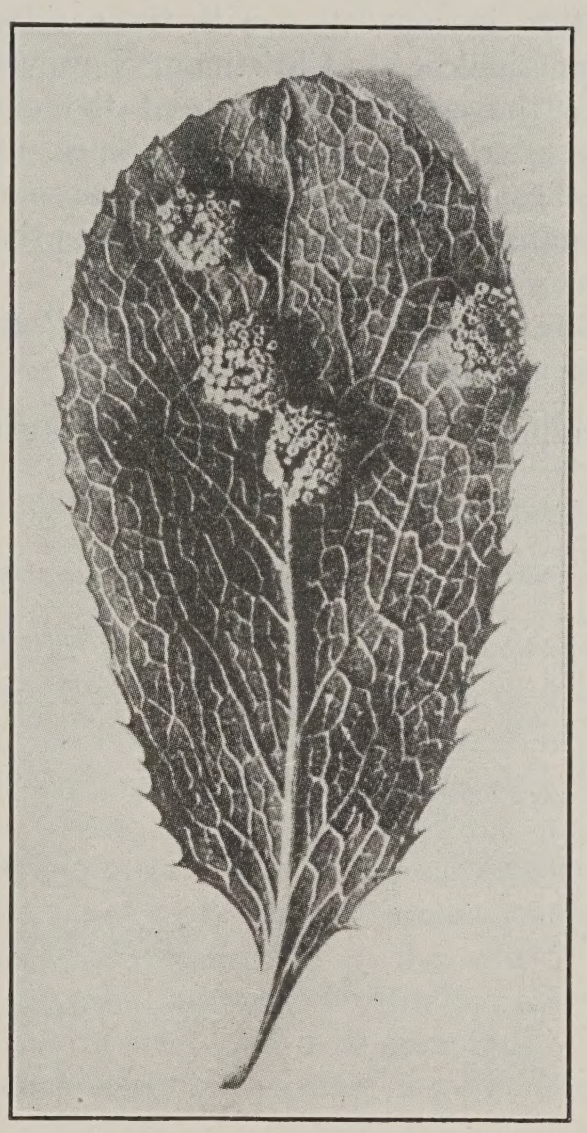


FIG. 346.—*Puccinia graminis.* Four pustules of aecia which have broken through the lower epidermis of a Barberry leaf. (After Buller.)

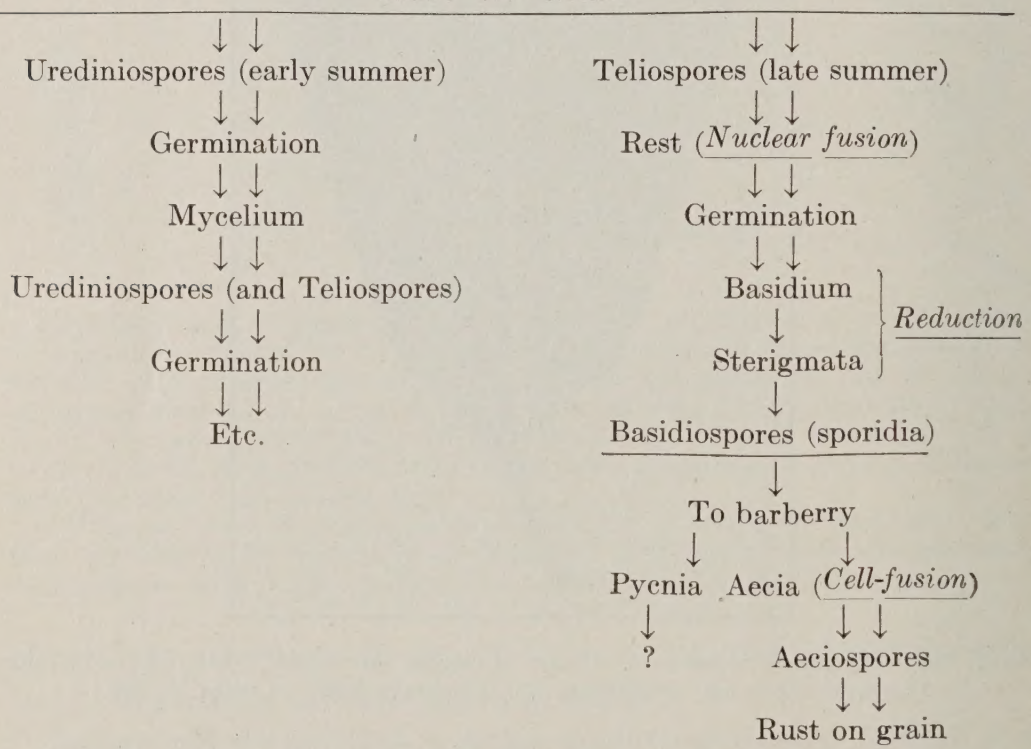
With these facts and figures in mind it is easy to understand how the rust disease may spread with great rapidity and be very difficult to keep under control.

In addition to the aecia, the mycelium develops within the leaf a reproductive structure called the *pycnium* (*pycnidium* or

spermagonium), which breaks through the *upper* epidermis and produces innumerable *pycniospores* (*spermatia*). The real nature of this structure is not definitely known. Studies by V. H. Blackman (and others) have led to the conclusion that the pycniospores "are male cells which formerly took part in a process of fertilization in connection with the aecidium, but have now become functionless,"[1] Christman,[2] however, inclined to the view that "the spermatia represent the once functional asexual spores of the gametophyte." Since nuclear fusion occurs in the teliospores, and since the pycniospores have been observed to germinate (like asexual spores), they should no longer be considered as sexual spores.

Diagram of Life History.—The life history of *Puccinia graminis* may be outlined as follows:

Outline of Life History of Wheat Rust



Physiological Forms.—Many of the various species of *Puccinia* and of other parasitic fungi have been found to comprise a number of different strains or races which, with minor exceptions,

[1] Blackman, V. H. Ann. Bot. **18**: 363. 1904.

[2] Christman, A. H. Bot. Gaz. **44**: 93. 1907.

appear to be identical in structure, but which are able to grow on only certain host plants and not on others. These strains have been variously called biological species, biological races, physiological species, biological forms, etc. Thus, for example, Freeman and Johnson,[1] working with *Puccinia graminis*, found four specialized races of that species, namely: *Tritici* on wheat, *Avenae* on oats, *Secalis* on rye, and *Hordei* on barley. About 37 specialized races are now known on wheat alone. Wheat rust can be transferred to barley and rye but not to oats; barley rust can be transferred to oats and rye; transfers can be made from rye to barley but not to wheat or oats; oat rust can be transferred to barley.

The specialization of some species varies in different countries. The discovery of this specialization is of very great importance for plant pathology, and is also of considerable theoretical interest for it may, as has been suggested, prove to be the first step in the origination or evolution of forms or species structurally different.

THE SMUT FUNGI

Ustilaginales

Habitat and Characteristics.—The smuts live as parasites (or alternately as saprophytes and parasites), chiefly on various species of the Grass Family, especially the cultivated forms such as corn, wheat, oats, barley, rye, sorghum, and others. The genus *Ustilago* is typical. The branching mycelium may extend throughout the plant body, but it commonly comes to fruit in the floral parts, and particularly in the ovaries. It grows not only between the cells, but may also send out haustorial branches which pierce the cell-walls and thus grow into or through a cell. When an infected plant is a perennial and dies down in the winter, the perennial mycelium of *Ustilago* remains alive in a resting stage in the underground parts, resuming its growth again in the spring into the new shoots. *Ustilago violacea* was observed by De Bary[2] to persist for more than ten consecutive years in

[1] The rusts of grains in the United States. U. S. Dept. Agr. Bur. Plant Ind. Bull. 216. 1911.

[2] De Bary, Heinrich Anton. Born at Frankfurt-am-Main, Germany, January 26, 1831; died at Strassbourg, January 19, 1888. Founder of modern mycology, and the first to prove that the substance of *Myxomycetes*

a plant of Soapwort (*Saponaria officinalis*) growing in the Botanic Garden in Freiburg.

FIG. 347.—Loose smut of wheat (*Ustilago tritici*). At the left, a normal head; the head beside it shows, at the tip, a few normal spikelets that escaped infection. Every spikelet of the other three heads is infected. (After G. M. Reed.)

LOOSE SMUT OF WHEAT

The following outline of life-history applies to the Loose Smut of Wheat (*Ustilago tritici*).

(p. 514) is protoplasm. First to describe the phenomenon of alternate hosts (*heteroecism*) in the life history of the plant rusts. Author of important botanical books and papers.

Mode of Infection.—The spores produced on a smutted plant (Fig. 347) form a copious dark brown or black dust that is easily blown about by the wind. Each spore is of a dark olive color with a spiny surface which enables it to adhere readily to any surface on which it alights. Countless spores are formed by each infected plant, and some of them, blown away, are almost certain to lodge on the inflorescences and other parts of nearby plants. Those that lodge on the stigmas germinate, and the mycelium grows down through the style and ovary to the ovules, where it remains dormant *in the embryo of the seed* until the seed is planted and germinates. It is of interest to read the description of this mode of infection in the words of Brefeld,[1] who (with the cooperation of Falck) was one of the first to demonstrate it:

"The germs of infection which penetrate to the young ovaries remain hidden in these . . . Not one trace may be seen outwardly on the infected and harvested seed of any smut infection which has already taken place . . . Only in the germination of the seed can the fungus develop further, in order later, at the time of blossoming, to cause, as if by a stroke of magic, the appearance of spore masses in the plant which, until then, had seemed healthy. The adaptation of a parasite to its host plant appears here with a completeness not known in any other case in the plant kingdom . . . It has been definitely proved by blossom infection that smutted individuals in the blossoming grain field form the center of infection for the plants and of the further distribution of the smut."

Spore-germination.—The spores retain their power of germination for only a few months. The germination resembles that of the teliospores of the Rusts. Under suitable conditions of temperature and moisture the spore puts forth a longer or shorter germ-tube called the *promycelium*,[2] which becomes copiously

[1] Brefeld, Oscar. Investigations in the general field of mycology. Part XIII Smut fungi (Hemibasidia IV). English translation by Frances Dorrance. Privately printed and distributed, 1912.

[2] Brefeld interpreted the promycelium as an imperfect or primative basidium which he called the *hemi-basidium*, and interpreted it as representing an intermediate stage in the evolution of the Basidiomycetes from some other group. On this basis he classified the Uredinales and Ustilaginales as *Hemi-basidiomycetes*.

branched. Thus the promycelium develops directly into a mycelium which penetrates and largely consumes the tissues of the floral organs within which spore-formation takes place, as follows (Fig. 348).

Spore-formation.—The spore-forming hyphae, *which have finally reached the floral organs* of a plant infected from seed, become enlarged and much branched. Then the walls of the hyphae become gelatinized, and the hyphae are divided into

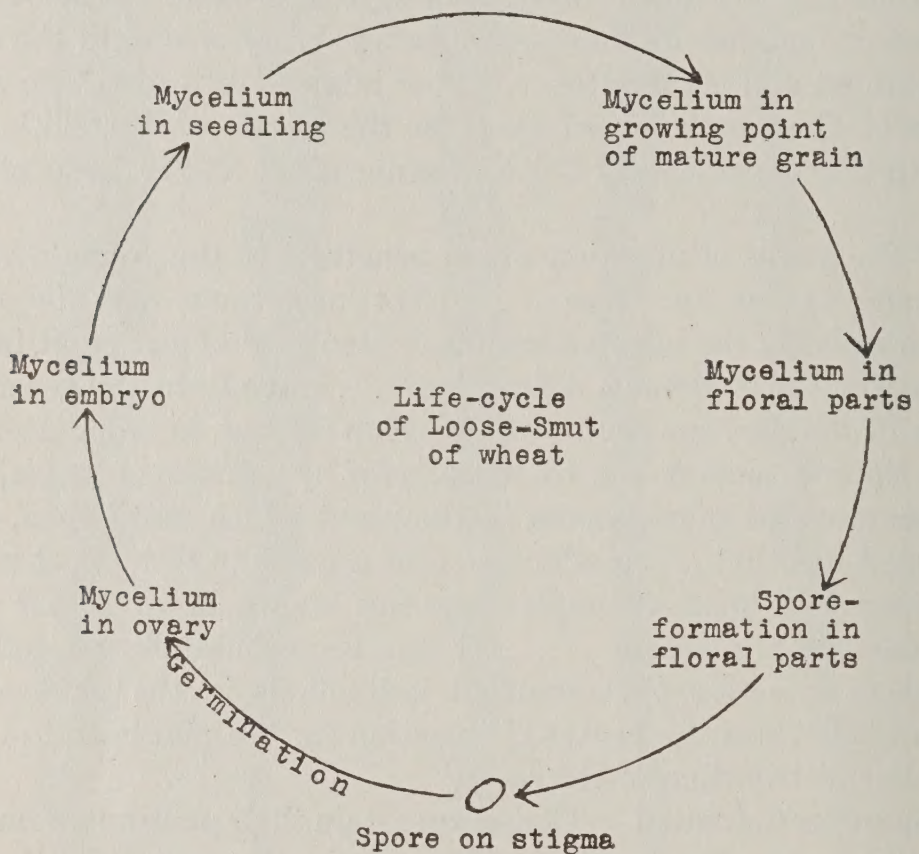


FIG. 348.—Diagram showing the life-cycle of Loose Smut of Wheat.

short cells by the formation of cross walls; these cells are the young spores. All trace of the individual hyphae is now lost, and the spores lie in the gelatinous mass formed from the walls of the hyphae. As the spores mature they assume their dark color, and their outer covering develops the characteristic tiny spines. When the gelatinous mass gradually disappears the spores lie loose forming the powdery black dust—the so-called smut, which is blown away by the wind to other plants, leaving only the stem portions of the inflorescence. All parts of the

flower are entirely destroyed in the process of spore-formation which completes the life-cycle (Fig. 348).

STINKING SMUT OF WHEAT

(*Tilletia tritici* and *T. laevis*)

The Stinking Smut or Bunt of wheat (Fig. 349) is a species of another genus of the Ustilagineae. The brief sketch of this life history given by McAlpine[1] gives such a vivid picture and is such an excellent example of clear, concise scientific description that it is quoted below.

"If we follow the spore of the Stinking Smut of wheat from the time it is shed until it reaches a fresh plant next season the way in which the disease is carried from season to season will be evident. In a district where this smut occurs, the sound grain may receive the spores by means of the wind or in the threshing machine, and this seed with the adhering spores may be sown in the same or in another district and thus introduce the disease. The grain in due course germinates, and the self-same conditions which are favorable to the germination of the wheat also suit the smut

FIG. 349.—Bunt or stinking smut of wheat (*Tilletia laevis*) on common wheat. At the left, infected head, and (below) smut balls which have replaced the grains of wheat. At the right, normal head and sound grains. (After G. M. Reed.)

[1] McAlpine, D. The smuts of Australia. Dept. of Agr., Melbourne, Australia. 1910.

spores. They readily germinate with moisture and produce secondary spores, or conidia, which in turn put forth delicate threads, and these readily enter the young wheat seedling. (Fig. 350.) There they soon reach the growing point of the stem and continue to grow—plant and parasite being supplied with food from the same source. Under ordinary conditions of growth the wheat-plant is able to provide sufficient food material for

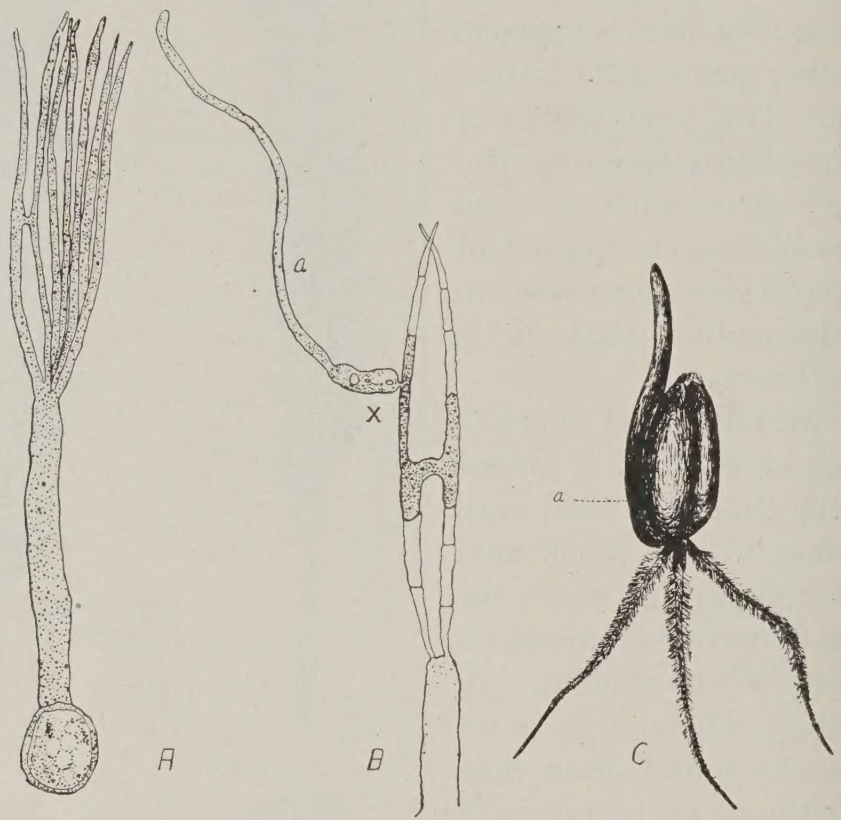


FIG. 350.—Bunt or stinking smut of wheat (*Tilletia tritici*). *A*, germinating spore producing, at the tip of the germ tube, more spores (sporidia), *B*, sporidia which have united; one has produced another spore (secondary spore or conidium) at x, and this is sending out an infection thread which infects the young sprouting wheat plant at *a* in *C*. (After Freeman and Stakman. Minnesota Agr. Exp. Sta. Bull. No. 122. 1911.)

both, and this goes on until the flower is formed and the young ovary begins to develop. Then the plant ceases to manufacture fresh material and transfers what has already been accumulated to the grain, for the benefit of the young and growing embryo. Here the fungus luxuriates in the rich supply of food and the filaments increase, multiply, and divide into innumerable branches, from each of which spores are formed; the wall of the filaments

becoming gelatinous. The wall soon deliquesces and is absorbed by the growing spore, which soon assumes its firm black covering; and what was at first intended as a store-house of nourishment for the embryo has been converted into a charnel house, densely packed with the spores of the overmastering fungus. These spores again reach the sound grain and repeat the process in the succeeding crop. The principle on which the treatment for the prevention of this smut is based, may be clearly seen from this brief account, for if the spores on the grain are destroyed, or their germinating power arrested, they will not be able to infect the young seedling and produce the disease."

The wide dissemination of spores by wind may be inferred from the fact that visible clouds of dust, coming from threshing machines during a run from a smutted field of stinking smut, have been found to be composed largely of spores. These are seen to be carried away by the wind. Wind-dissemination has also been demonstrated by microscopic examination of washings from the foliage of plants widely separated and remote from the grain field, and again by counting the number of spores that fall on spore-traps located at a distance from the field. The spore-traps are properly supported plates of sterilized nutrient agar, or crystallizing dishes containing sterilized water. After the traps have been exposed in the field for a given period they are removed to the laboratory and the spores counted.[1]

Heald and George found that the average number of spores on leaves of apple trees ran as high as 145,000 and more per leaf. The trees were at least a half mile from any wheat field, and much further from any threshing operation. The number of spores falling on the surface of a spore trap averaged nearly 6,000 per square inch at a distance of a quarter of a mile from the nearest wheat field, and about one mile and a half from the nearest thresher. Between August 16, and October 31, 1916, more than 5,000,000 spores fell on each square foot of surface.

LOOSE SMUT OF OATS (USTILAGO AVENAE)

Life History.—The spores of Loose Smut of oats are, like those of Loose Smut of wheat, formed in the ovary by a method similar

[1] Heald and George. The wind dissemination of the spores of bunt or stinking smut of wheat. State Coll. of Washington, Agr. Exp. Sta. Bull. 151, Dec., 1918.

to that described above for Loose Smut of wheat. In rare cases the smut has been found on the leaves and anthers. The method of infection is wholly unlike that in Loose Smut of wheat. The ripe spores may lodge either on the surface of ripe grains or in the soil. In either case the conditions that favor the germination of the seed also favor the germination of the spores.

In the method of spore-germination the Loose Smut of Oat also differs from that of wheat. The spores commonly germinate in the soil. The promycelium produced from the spore becomes divided into (usually) four cells. From each cell a tiny lateral bud is formed, and one is also generally formed at the apex (Fig.

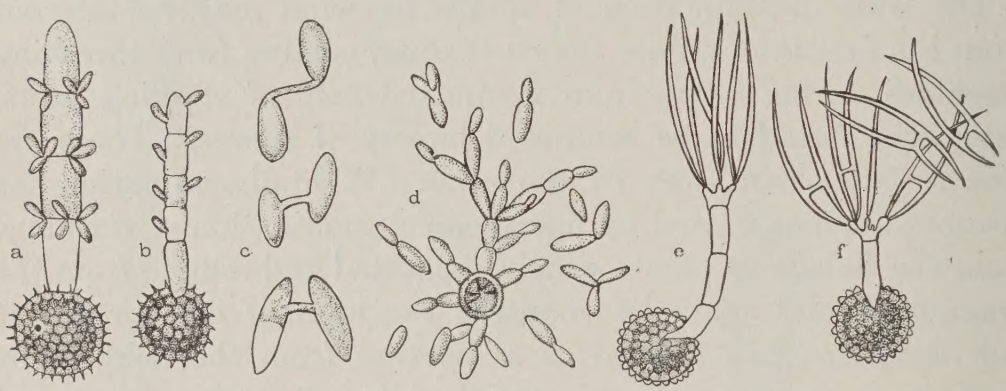


FIG. 351.—*a*, *Ustilago kühneana*, spore germinated, showing the promycelial spores (conidia) in whorls on the promycelium (after Brefeld); *b*, *U. scabiosae* on *Scabiosa arvensis*, twelve hours after germination in water; *c*, promycelial spores conjugating; *d*, *U. segetum*, a yeast-spore colony produced from a single spore (After Brefeld); *e*, spore of *Tilletia tritici* (Bunt of Wheat) germinating after 48 hrs. in water; *f*, the same more advanced, showing the H-shaped sporidia, two of which have already fallen away from the promycelium. (All figures redrawn from Plowright.)

351, *b*). In *Ustilago Kühneana* the conidia are formed in whorls (Fig. 351, *a*). These buds are called *conidia*.[1] Commonly all the protoplasm of the promycelial cell flows into the conidium which, when mature, usually falls away. In some cases the primary conidium gives rise, by budding, to a secondary conidium and this may be further repeated, producing a series of buds in a manner similar to vegetative reproduction of yeast. For this reason the conidia have been called *yeast-spores* (Fig. 351, *d*). Under certain conditions two or more conidia may fuse before they germinate. The conidia may live for a time and increase saprophytically in the soil, but their virulence rapidly decreases

[1] The conidia (Brefeld's name for them) were called by De Bary *sporidia*. They have also been called *promycelial spores*.

and, at the end of a few weeks they have practically lost the power to infect. Only conidia are formed in the soil, and only spores within the ovary. Thus there is an alternation of the parasitic and the saprophytic habit. When contaminated oats are planted the young seedling becomes infected, as follows:

When the conidia on the surface of the germinating grain germinate the germ-tube enters the seedling, usually through the delicate tissue at the junction of the roots and stem. The

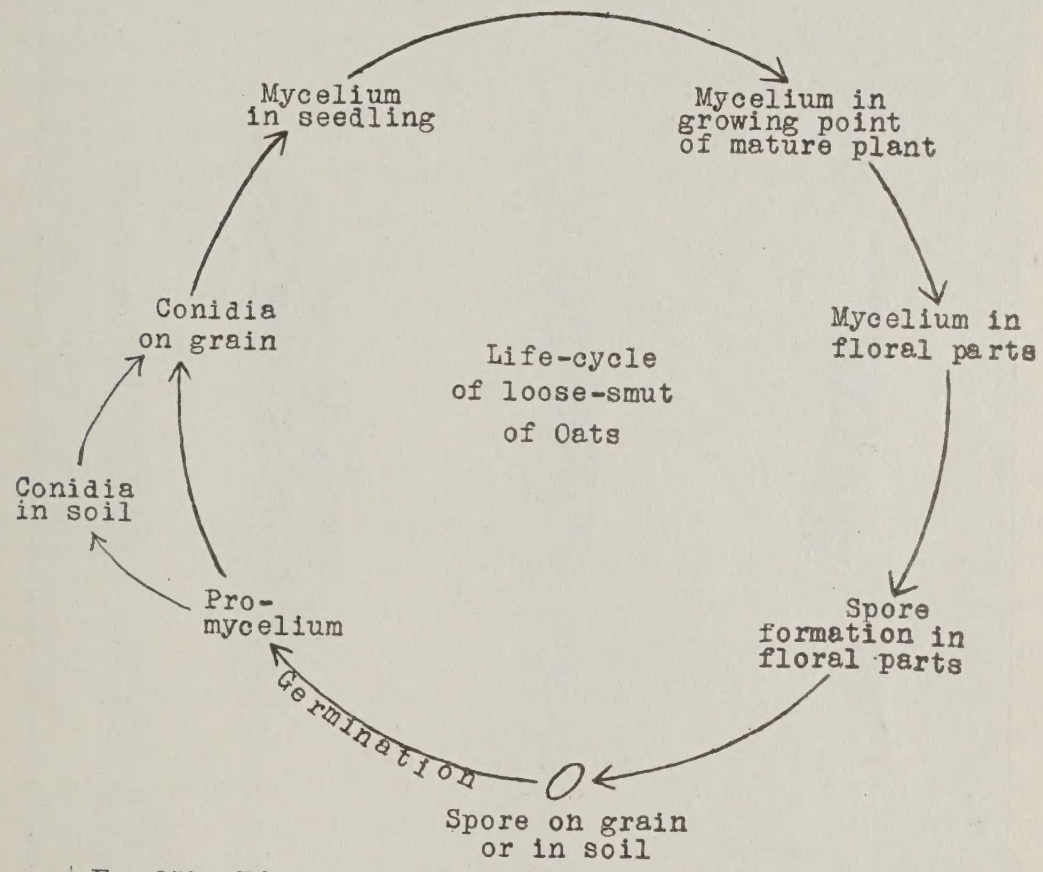


FIG. 352.—Diagram showing the life-cycle of Loose Smut of Oats.

mycelium soon reaches the tender nutritious cells of the growing-point at the tip of the stem where it is carried along as the stem grows in length. The older the seedling at the time of infection the longer is the stem and therefore the less are the chances for the mycelium to reach the tip. When the terminal inflorescence is formed, the mycelium passes into its branches and ultimately into the ovaries, producing the smut or mass of spores like those with which we started, thus completing one life cycle and initiating another (Fig. 352).

COVERED SMUT OF BARLEY

There are two smuts common on barley—the Naked Smut (*Ustilago nuda*) and the Covered Smut (*Ustilago hordei*). The life history of the former is similar to that of the Loose Smut of

Fig. 353.—Covered Smut of Barley (*Ustilago hordei*). (After G. M. Reed.)

wheat, infection taking place in the flower, and the promycelium giving rise directly to mycelia within the ovary, causing seed infection without the formation of conidia.

In the Covered Smut (Fig. 353), infection takes place in the seedling and the spores are formed within the ovary. They have a *smooth* surface but, in contrast to the Loose Smut, when the spores are ripe they remain as a hard mass within the wall of the ovary which does not burst as in the case of the Loose Smuts. In germination the spores produce a four-celled promycelium which bears conidia at the sides and apex. The conidia manifest yeast-like budding and are active in spreading the disease.

Modes of Smut Infection.—Four different modes of smut infection are recognized (including those described above) as follows:[1]

1. *Seedling Infection.*
   a. From spores adhering to the surface of the grain, as in Loose Smut of oats (*Ustilago avenae*).
   b. From spores in the soil in which the grain is planted (*Soil infection*), as in Flag Smut of wheat (*Urocystis tritici*) and others.
2. *Local infection* in any young or growing tissue. The mycelium remains localized where the infection takes place; *e.g.*, Corn smut on maize (*Ustilago maydis*). In the case of maize the spores from an ear, tassel, or other part, infected with smut live saprophytically in the soil and produce conidia. When they germinate the mycelium may enter any young tender tissue of roots, stem, leaves, or flowers. Conidia may be formed at the surface of the soil, and these, blown by the wind, may lodge on the staminate or pistillate flowers or other parts and thus cause *Local infection.*
3. *Flower infection*, which may take place through the stigma or by the germ-tube penetrating through the wall of the ovary. The mycelium produced in the ovary from the promycelium lies dormant in the embryo of the ripe grain, grows throughout the entire plant developed from the infected grain until it reaches the flowers where the spores are produced in the ovary, *e.g.*, Loose Smut of wheat (*Ustilago tritici*) and Naked Smut of barley (*Ustilago*

[1] Based upon McAlpine's summary.

nuda). Confined largely to the Loose Smuts, whose spores are readily disseminated by the wind.

4. *Shoot infection,* which takes place at the base of the young shoots formed in "tillering," as in the infection of the perennial rye (*Secale montanum*) by *Urocystis occulta.*

The known facts concerning the modes of infection of various crop plants by smut required the painstaking observation and experiments of many investigators extending over a period of more than one hundred years.

Transformation of Sex by Smut Infection.—The Anther Smut (*Ustilago violacea*) infects the Campion (*Lychnis dioica*), which is dioecious. It produces its violet spores only in anthers. When the pistillate plants are infected they are stimulated to produce stamens in which the spores develop, while the formation of pistils is inhibited. The means by which this is brought about is not understood.

CORN SMUT

The smut of Indian Corn (*Ustilago Zeae*) attacks all organs of the plant, but is confined to young and growing parts where there is embryonic tissue. It is frequent on stem, leaves, tassel, and cob (Fig. 354), but has been found only rarely on the roots.

Mode of Infection.—In the cereal smuts above described the infection is *systemic,* that is, it spreads through the tissues of the host plant from the point of infection, producing spores at points remote from the point of initial infection.

In the corn smut the organism does not spread from the place of infection, and in this respect it differs more or less from the smuts of other cereals. In the axil of each of the lower leaves of the corn plant below the ear-node there is a bud, and the embryonic tissue of these buds is readily attacked by the spores of the smut. As Potter and Melchers[1] have pointed out, "a common mode of infection is the development of a virulent culture in moisture held in the axil of a leaf of a young plant. Such a local culture is likely to produce other infections in adjoining nodal tissues and thus produce a pseudosystemic development of the disease."

[1] Potter, Alden A. and Leo E. Melchers. Study of the life history and ecologic relations of the smut of Maize. Jour. Agr. Res. **30**: 161–173. Jan. 15, 1925.

About three weeks are required from the date of infection to the maturing of the "smut-boils" and the formation of spores.

Comparison of Cereal Smuts.—The life histories of the various cereal smuts are briefly shown in the following table of comparison (p. 500).[1]

Crop Losses from Smut.—It will readily be recognized how extremely difficult it is to get rid of smut after the soil of a field or a crop of seed has once become infected. In the latter case the infection is spread to clean seed in the threshing machine. The

FIG. 354.—Corn-smut (*Ustilago maydis*) on stalk, tassel, ear, and leaf of *Zea Mays*.

difficulty of control is increased by the enormous number of spores produced. They are so small that it has been estimated that it would require about 25,000,000 to cover a square inch of surface. Probably as many as half a billion to a billion spores are produced in an infected head of wheat; each grain may carry on its surface several millions.

The annual loss to various grain crops in the United States alone from smut infection amounts to a large percentage of the entire crop—in some cases to total loss. The loss of wheat from Stinking Smut was estimated at 10,500,000 bushels in 1921; in

[1] The table is simplified from McAlpine, *l.c.*, p. 68.

TABLE X.—COMPARISON OF CEREAL SMUTS

Cereal	Kind of smut	Scientific name	Germination of spores	Dispersion of spores	Mode of infection
Wheat	Stinking smut	Tilletia tritici and Tilletia levis	With promycelium and crown of conidia	Threshing time	Seedling
	Loose smut	Ustilago tritici	Directly forming mycelium	Flowering time	Flower infection
	Flag smut	Urocystis tritici	With promycelium and crown of conidia	In harvesting and threshing	Seedling and young shoots
Oats	Loose smut	Ustilago avenae	With promycelium and conidia	Flowering time	Seedling
Barley	Naked smut	Ustilago nuda	Directly forming mycelium	Flowering time	Flower infection
	Covered smut	Ustilago hordei	With promycelium and conidia	Threshing time	Seedling
Maize	Head smut	Sorosporium reilianum	With promycelium and conidia	Flowering time	?
	Corn smut	Ustilago zeae	With promycelium and conidia	At all times during growth of plant	All young and growing parts

1918 it was estimated at 19,063,000 bushels. During the four year period 1917–1920 the loss from corn smut averaged about 80 million bushels annually or nearly 3% of the average crop.

Series II. Eubasidiomycetes

A FLESHY FUNGUS (AGARICUS)

Habitat.—Fleshy fungi are found widely distributed, growing in the soil of fields, pastures, and woods, or on tree trunks, decaying logs, and elsewhere. The familiar edible mushroom (*Agaricus campestris*), as its name implies, grows commonly in meadows,

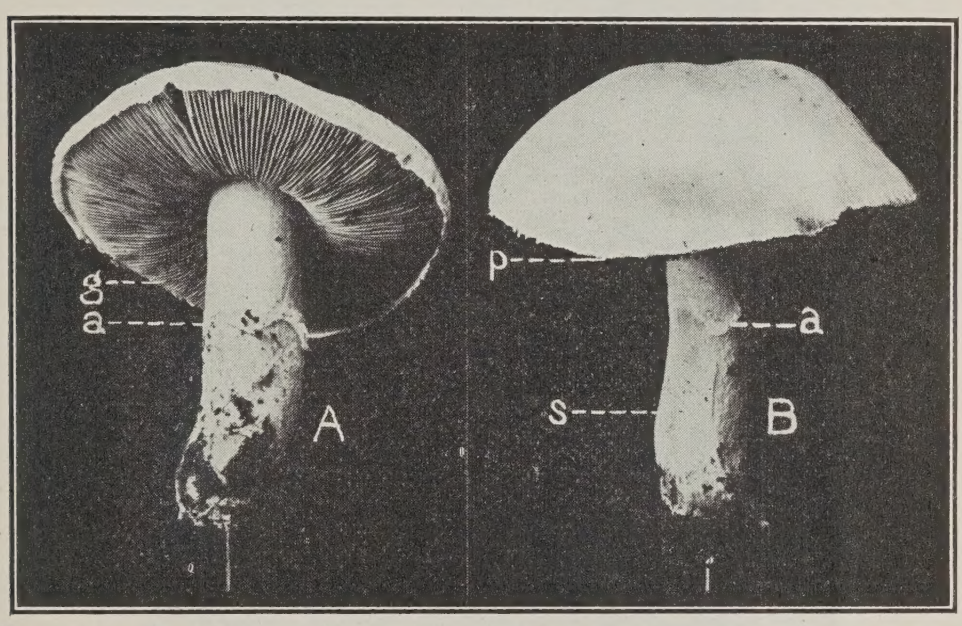


FIG. 355.—Meadow mushroom (*Agaricus campestris*). *A*, view showing under side of pileus; *g*, gills; *a*, annulus, or remains of the veil attached to the stipe; *B*, side view; *s*, stipe; *a*, annulus; *p*, margin of pileus, showing at intervals the remains of the veil. (After W. A. Murrill.)

and is hence often called the "meadow mushroom" (Fig. 355). One of the most poisonous species, *Amanita phalloides*, (Fig. 356), resembles *Agaricus* superficially and is often mistaken for it.[1] *Amanita* always has, at the base of the stalk, a *cup*, which *Agaricus* lacks.

Description.—The body of *Agaricus* consists of a short fleshy stalk (the *stipe*), having numerous root-like hyphae (*rhizomorphs*)

[1] *Amanita phalloides*, the "deadly amanita," is the fungus most commonly designated by the name *toadstool*, though that name is used indiscriminately for almost any poisonous form. The word is said to be derived from the German word, *todt* (death) + stool, and not from toad.

penetrating the soil from its lower end, and bearing at its upper end an umbrella-shaped expansion, the *pileus*. On the under side of the pileus are numerous thin lamellae or *gills*. The stalk and pileus are composed of innumerable hyphae (Fig. 357), closely associated together in a pseudo-tissue, but there is no real tissue-differentiation, such as occurs in the mosses and ferns

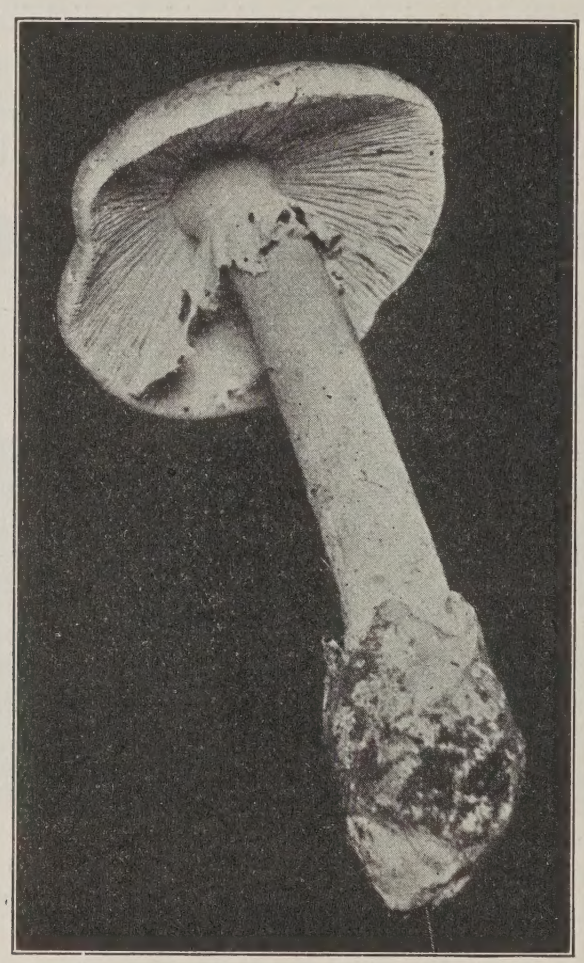


FIG. 356.—The deadly Amanita, *Amanita phalloides*. Note the cup at the base of the stipe. (Photo by E. M. Kittredge.)

and higher plants, though the external layer may usually be peeled off with ease.

Reproduction.—If the pileus of *Agaricus* is placed with the gills down over a piece of white paper, and left for a few hours, a dark purplish deposit will form in lines under each gill. With *Amanita* the color is white. This deposit (the "spore-print") is composed of spores, shed from the surfaces of the gills (Fig. 358). Microscopic examination discloses the fact that the gills are

composed of a net-work of hyphae. The surface layer of the gills (*hymenium*), when mature, comprises three elements.

1. *Basidia* (singular *basidium*), short, thick, club-shaped bodies filled with protoplasm, and, when mature, projecting slightly from the general surface. At the tip of each basidium are (in

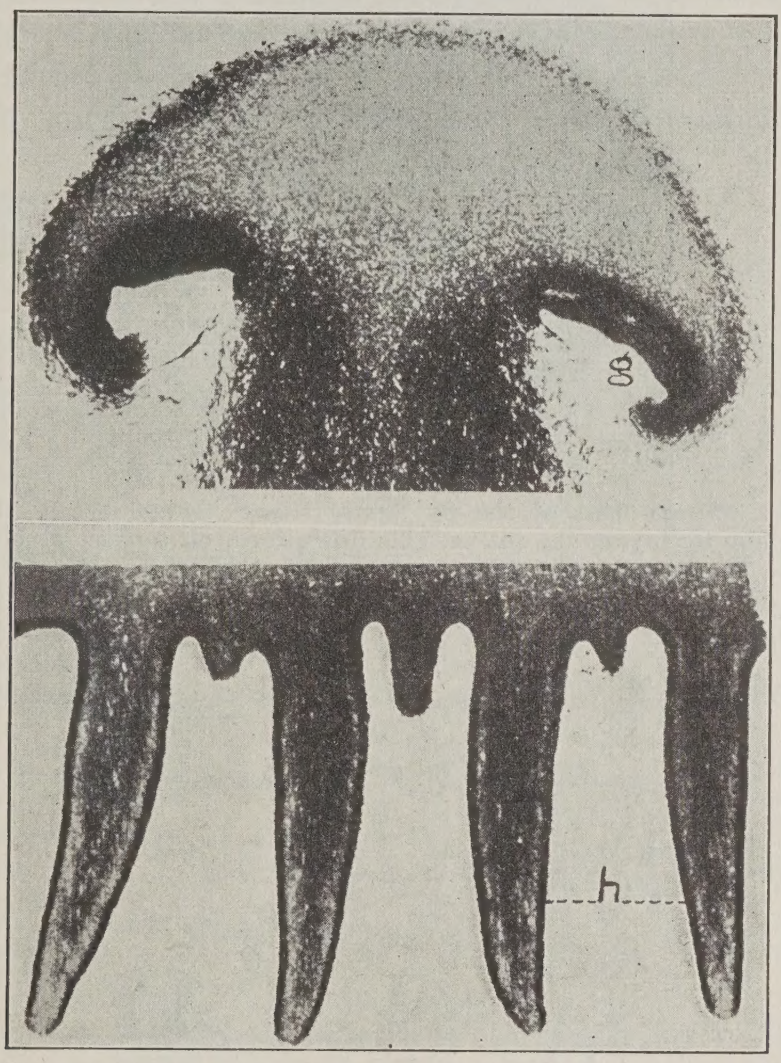


FIG. 357.—*Cortinarius cinnamomeus*. Above, longitudinal section through stipe and pileus, showing gills (*g*); below, longitudinal section through primary and secondary gills; *h*, hymenium or sporogenous surface. (After Gertrude E. Douglas.)

the cultivated agaric) two tiny projections, the *sterigmata* (singular *sterigma*), and at the end of each sterigma is borne a spore (*basidiospore*). In the wild agaric (*Agaricus campestris*) and in most of the species of the gill-bearing fungi there are four sterigmata, as shown in figure 359. The mature hymenium presents

basidia of various "generations," as Buller calls them—past, present, and future (Fig. 360).

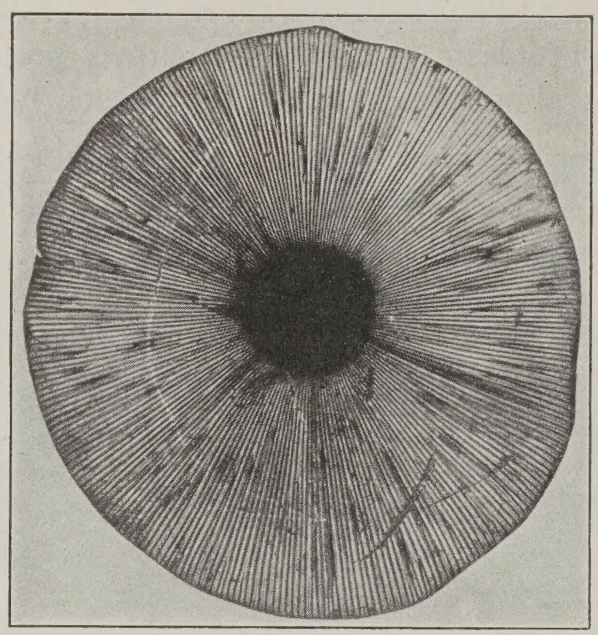


FIG. 358.—Spore-print of the fly agaric (*Amanita muscaria*). The spore-print is made by laying the pileus, gills downward, on a sheet of black paper. The white spores fall onto the paper, making the print. (Photo by W. A. Murrill.)

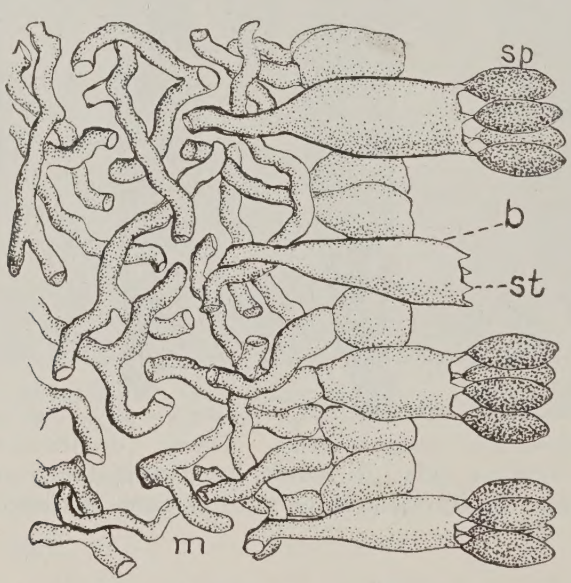


FIG. 359.—Fruiting surface (hymenium) of a mushroom (*Agaricus*). *m*, hyphae of the trama and sub-hymenium; *b*, basidium; *st*, sterigma; *sp*, spores. (Diagrammatic.)

2. *Paraphyses*, resembling immature basidia in appearance, but never bearing sterigmata nor spores.

3. *Cystidia*, sterile bodies, differing from the paraphyses in form and size. They are not present in *Agaricus campestris*, nor in numerous other species.

Beneath the hymenium is the *sub-hymenium* (Fig. 360), and beneath these two layers are the hyphae that compose the main substance of the gill—the *trama*.

Color of the Spores.—The young spores of *Agaricus campestris* are white and, therefore, at this stage the gills appear white.

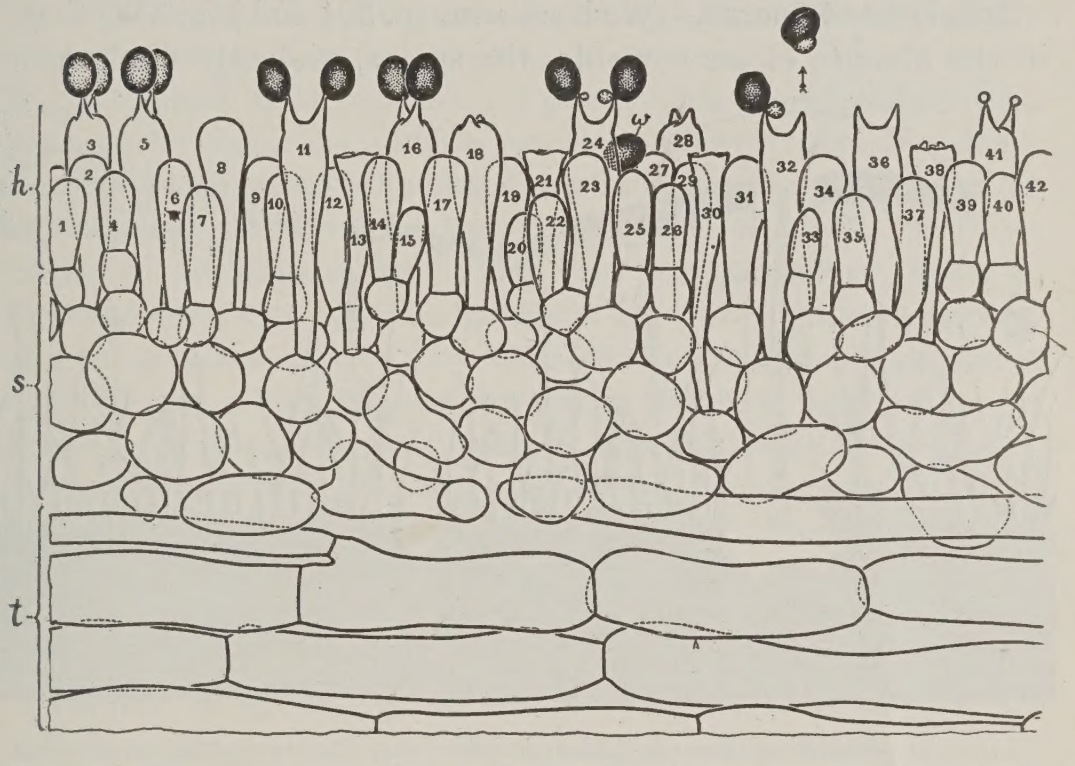


FIG. 360.—Meadow mushroom (*Agaricus campestris*). Microscopic view of part of a living gill showing the method of spore-discharge. (After Buller.)

Later the color changes to purplish and, at about the time the spores are shed, they become dark brown.

Discharge of Spores.—When the spores are ripe they do not, as a rule, merely "fall off" from their point of attachment, but are thrown off or discharged by a process which is characteristic for the species.[1] Just before a spore is to be discharged a drop of water begins to form by excretion at the point where the spore is

[1] The methods of spore discharge in Basidiomycetes have been worked out in beautiful detail by the painstaking studies of Buller, whose work has been freely drawn upon in these pages. Buller, A. H. Reginald. Researches on fungi. Vols. I, II and III. London, 1909, 1922, 1924.

attached to the sterigma (Fig. 360). This drop grows quickly to a maximum size when the spore is violently shot away, carrying the water drop with it. The time from the first appearance of the water drop until the spore is shot away is about 5 seconds. The drop of water adhering to the spore helps to make it adhesive, so that it readily adheres to any surface it may fall upon. The mechanism by which the spore is shot away is not, as yet, understood.

Dispersal of Spores.—We have seen (p. 504 and Fig. 358) that, in the absence of air currents, the spores, violently discharged

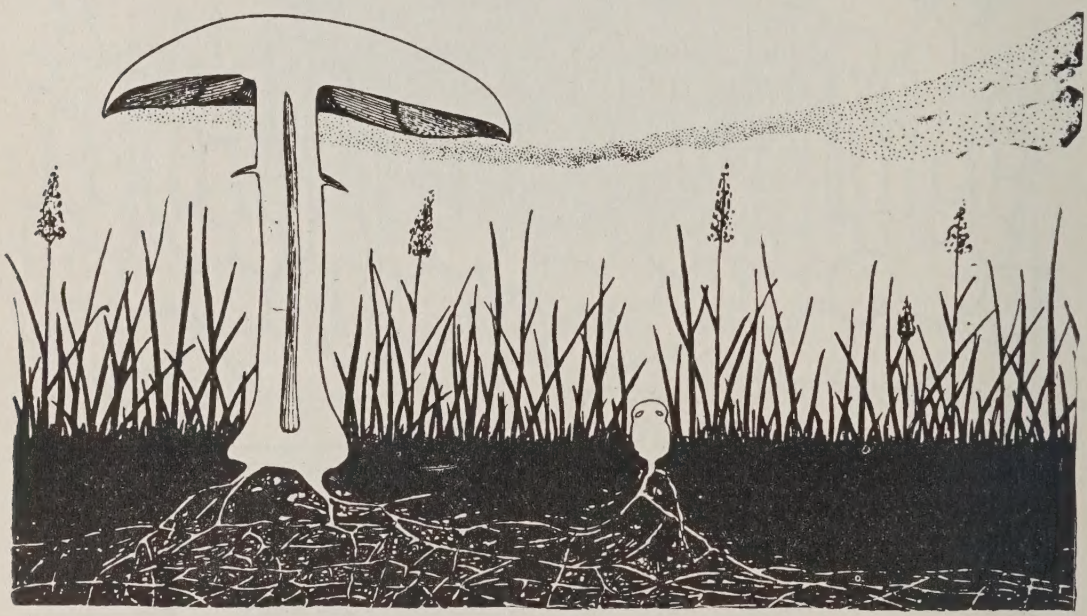


FIG. 361.—Horse mushroom (*Agaricus arvensis*), illustrating the manner in which the spores are dispersed. A slight lateral movement of the air is indicated as carrying the spore-cloud away from the underside of the pileus. Reduced slightly more than ½. (After Buller.)

from the hymenium, fall more or less vertically downward and will make a "spore print" on the surface underneath the pileus. In nature, however, the air surrounding the fruiting body is seldom, if ever, perfectly quiet; there are always gentle convection currents, even if the wind is not blowing appreciably. The pileus is raised well up above the surface by the growth of the stalk, and the spores, when discharged, being so very light and settling so very slowly, are wafted away more or less horizontally, and carried to considerable distances before they can fall to the ground (Fig. 361). Buller ascertained that the average rate of

fall of thistle-down (the tufted fruits of the Canada thistle) was 6.6 inches or 167.6 mm. per second, while the average rate of fall of the spores of the meadow mushroom was only 1.61 mm. per second. In other words, it requires 5.8 seconds for a spore to fall one inch.[1] This long suspension in air insures the transportation of the spores to relatively great distances by the wind.

Adjustments to Insure Distribution of Spores.—If a fresh fruiting body of the common mushroom is placed horizontally the stipe will shortly turn upwards through an angle of 90°, more or less, so as to bring the pileus again horizontal. This is a geotropic response to the stimulus of gravity, and its advantage is in keeping the pileus in a position most favorable for spore-discharge. The rapid elongation of the stipe in growth has the same biological significance. Buller notes two other means by which the most favorable adjustment is secured for spore-discharge, namely: the expansion of the pileus by which the gill-chamber is opened and the gills placed with their long axes horizontal, the geotropic sensitiveness of the gills themselves, by which, in response to the stimulus of gravity they will also, unless hindered, turn in such a way as to maintain themselves in a vertical plane.

Some species (*e.g.*, the Saddle-Back Fungus, *Polyporus squamosus*) are also sensitive to light, and react to that stimulus in a way to favor the best distribution of spores. The meadow mushroom, however, has not been found sensitive to the stimulus of light.

Number of Spores.—The number of spores produced by one individual fungus is almost beyond belief, and the task of ascertaining their number is far from easy. The number varies, of course with species, age, temperature, and other factors. There are usually several to many fruiting bodies to each individual plant. Computations made by Buller for certain fleshy fungi gave the following numbers of spores in one fruiting body.

Species	Number of Spores
Meadow mushroom (*Agaricus campestris*)...	1,800,000,000
Shaggy-mane (*Coprinus comatus*).....	5,240,000,000
A Polypore (*Polyporus squamosus*).....	11,000,000,000

In the case of the meadow mushroom as many as 40,000,000 fell during each hour of the spore-fall period, while the number

[1] Some of the bacteria (*e.g.*, *Streptococcus gracilis*) require over three hours to fall one inch in still air.

falling per hour was, for *Coprinus comatus*, 100,000,000. The average length of the spores discharged by the *Coprinus* was 12.55 μ. "placed end to end, therefore, they would stretch through a distance of forty-one miles!" But, says Buller, "Numerous as are the reproductive bodies of a Mushroom . . . they pale into insignificance compared with those produced by . . . the Giant Puff-ball" (*Lycoperdon giganteum* Hussey). The number produced in one fruit body was calculated to be about 7,000,000,000,000, "or as many as would be liberated by about 4000 good sized Mushrooms." This puff-ball measured $40 \times 28 \times 20$ cm. (approximately $16 \times 11 \times 8$ inches), being therefore only a moderate sized specimen. Buller asserts that a large specimen "which, it is said, may sometimes almost attain the dimensions of a sheep, is the most prolific organism living on our planet."

If we keep in mind the fact that each plant produces several fruit bodies in a year we shall see that the total number of spores *per plant* per year is beyond comprehension. Buller estimates it at 100,000,000,000 for *Polyporus squamosus*. The most prolific animals are fish, of which the most prolific known is the ling, which has been found to produce as many as 28,361,000 eggs in one year, or in 20 years, some 500,000,000 eggs. By comparing these figures with those for fungi we see that the fungi are, by all odds, the most prolific individuals of either plants or animals.

Obviously if all these spores germinated and came to maturity the surface of the globe could not contain all the fleshy fungi that would be produced in any one year. The fact is that the death rate is enormous, Buller having calculated that, for every spore that develops into a mature plant, something like one thousand billion spores are wasted!

Spores in High Altitudes.—Buller has noted that the air is often so full of the black spores of certain Hymenomycetes, that if their diameters were increased by only 100 times, without their rate of fall being also increased, "we should see them with the naked eye, and they would often darken the air and astonish us with their vast numbers and extraordinary variety."

In connection with investigations of the general spread of rust disease, the Office of Cereal Investigations of the U. S. Department of Agriculture has recently made studies of the dissemination

of spores by air currents at high altitudes.[1] The method was to expose spore traps on the wing struts of an airplane. It was found that pollen-grains and spores of various kinds (including urediniospores and aeciospores of *Puccinia graminis*) are very numerous up to a height of two miles, but relatively scarce at greater altitudes.

Of course, the important thing to know is not whether spores occur at such great altitudes, but whether spores that might fall from such heights are capable of germination so that plant diseases may be disseminated in that way.[2] The investigations just cited showed that urediniospores caught as high as 7000 feet germinated readily, but further studies are needed before conclusions will be justified as to the spread of plant diseases by spore-dissemination at high altitudes.[3]

Sexuality in the Hymenomycetes.—Sexuality in the Hymenomycetes is reduced to its lowest terms, being confined to nuclear phenomena. The steps in the process, first clearly outlined by Wager[4] in 1891 and later by Ruhland,[5] are in brief as follows. At a very early stage in the development of a basidium two or more nuclei pass into it from the hypha that bears it. These nuclei fuse to form one nucleus, which increases in size and then divides, forming two nuclei. Each of these daughter nuclei then divides, thus giving rise to four nuclei in the basidium. While the sterigmata are forming, these four nuclei pass to the basal part of the basidium and remain in close contact. Subsequently each nucleus passes to the base of a sterigma, which has now begun to form a spore on its tip. The diameter of the sterigmata is much less than that of the nuclei, but the latter become sufficiently elongate and slender to enable them to pass through the sterigmata and into the spores. After entering the

[1] Stakman, E. C., and others. Spores in the upper air. Jour. Agr. Research. **24**: 599–606. May 19, 1923.

[2] Rain would be one of the important agencies in bringing the spores from high altitudes to the ground.

[3] It is also known that fungal spores and bacteria occur in considerable numbers on the surfaces of pollen-grains, and are thus transported to considerable distances on wind-borne pollen (*Cf.* p. 380, *et seq.*).

[4] Wager, Harold. Ann. Bot. **6**: 146–148. 1892. See also Ann. Bot. **7**: 490–514. 1893; **8**: 323–334. 1894.

[5] Ruhland, W. Botanische Zeitung. **59**: 187–206. 1901.

spores each nucleus divides into two, so that the spores are *binucleate*. The details of these processes are shown diagramatically in Fig. 362.

Although the nuclear fusion in the basidium of the Basidiomycetes has been interpreted by some investigators as a true

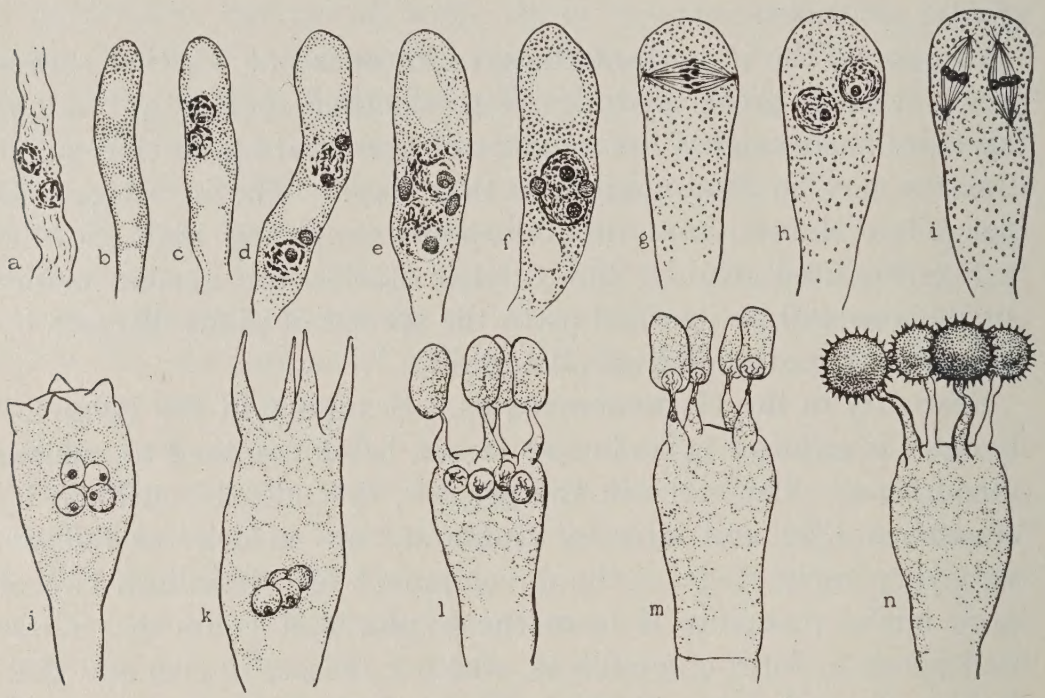


FIG. 362.—Development of basidium and spores in a Hymenomycete. *a-n*, successive stages. *a*, portion of hypha from a gill, with two nuclei; *b*, young basidium, without nuclei; *c*, young basidium with two nuclei which are considered to have passed into it from the hypha; *d*, slightly older basidium with two nuclei larger than those in *c*, and each of which was probably formed by the fusion of two nuclei similar to those in *c*; *e*, two nuclei similar to those in *d* are beginning to fuse. The small bodies beside the nuclei are *archoplasmic* bodies or centrospheres, from which are developed the *spindle fibers* and *centrosomes* concerned in nuclear division; *f*, basidium with nuclear fusion complete; *g*, a fusion nucleus, such as that in *f*, undergoing division. The centrosomes at the poles of the spindle, and the spindle fibers were derived from the centrospheres shown in *f*. The chromosomes appear on the equator of the spindle; *h*, two daughter nuclei resulting from the nuclear division in *g*; *i*, the daughter nuclei dividing; *j*, basidium with four nuclei. Four sterigmata are just beginning to form; *k*, later stage than *j*; *l*, young spores forming at the tips of the sterigmata. The four nuclei have moved up to the bases of the sterigmata; *m*, the nuclei have passed through the sterigmata and are entering the spores; *n*, each sterigma bears a mature spore with characteristic wall. (The figures are more or less diagrammatic. *a-k* are based upon Wager; *l-n*, upon Ruhland.)

sexual fusion, others are more cautious. The exact significance of this fusion is not yet entirely clear, but, even when three or more nuclei fuse, the conclusion seems warranted that the fusion takes the place of the union of true gametes in other forms, and

is, therefore, *physiologically* equivalent to fertilization, causing invigoration of the spores.

Outline of Life History of Meadow-mushroom

Spore (Basidiospore)
↓
Mycelium
↓
Binucleate cells
↓ ↓
Young Sporophore ("Buttons")
↓ ↓
Mature sporophore (the "Mushroom") { Stipe / Pileus
↓ ↓
Gills
↓ ↓
Hymenium
↓ ↓
Basidium (*Nuclear fusion*)
↓ (*Reduction*)
Sterigma
↓
Spore (Basidiospore)

Vegetative Propagation.—The meadow-mushroom is propagated for food from "bricks" of mycelium, or "spawn" that may be purchased from seedsmen. When portions of these "bricks" are placed in suitably prepared soil, under favorable conditions of moisture and heat, the mycelium resumes its growth, ramifying in all directions through the soil. At numerous points on the mycelium tiny little "buttons" form (Fig. 363). As the buttons enlarge, a little chamber forms near the tip (Fig. 364), and into this chamber some of the hyphae grow, forming the "gills," with their "fruiting" surface. While the gills are forming, other hyphae form a *veil*, extending from the stipe to the edge of the pileus, and protecting the gills until the spores are ripe. By continued growth of the pileus the veil becomes ruptured, thus allowing the spores to escape.

Entire new mushrooms may also be obtained by growing pieces of a young plant on suitable nutrient media. From such pieces mycelium is produced which ultimately bears the "buttons."

Other Groups of Fleshy Fungi.—In addition to the gill-bearing fungi (Agaricaceae), there are (as noted on p. 479) five other

families of Basidiomycetes: the Polyporaceae (Fig. 365), the Hydnaceae, the Thelephoraceae: the Clavariaceae, and the

FIG. 363.—The meadow mushroom (*Agaricus campestris*, var. *Columbia*). Young fruiting bodies (carpophores). The mycelial hyphae are in the substratum. (Photo by G. F. Atkinson.)

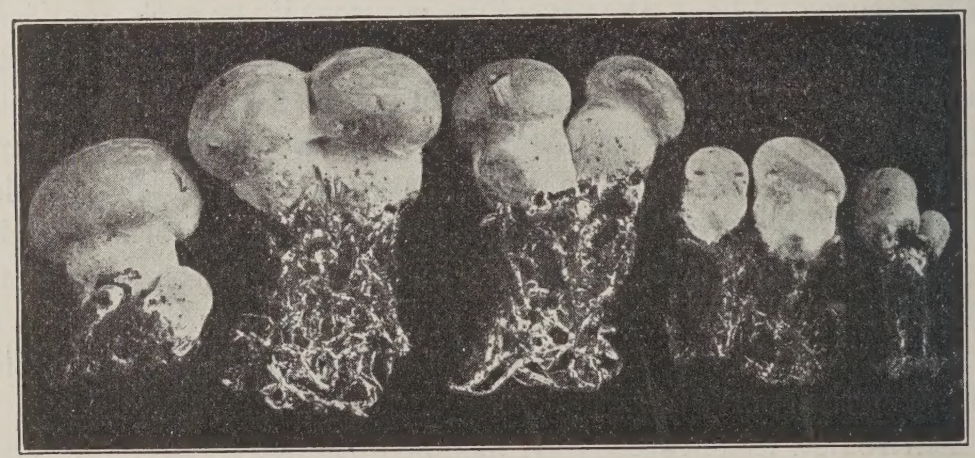


FIG. 364.—The common mushroom (*Agaricus campestris*). Young "buttons." (Photo by G. F. Atkinson.)

Tremellineae. The common "puff-balls" are Gasteromycetes, with the fruiting surface entirely enclosed in the more or less

globular fuiting body, almost the entire contents of which break down into the powder or dust of the ripe puff-ball (Fig. 366).

FIG. 365.—A pore-bearing fungus (*Polyporus betulinus*). Under (fruiting) surface, showing the pores.

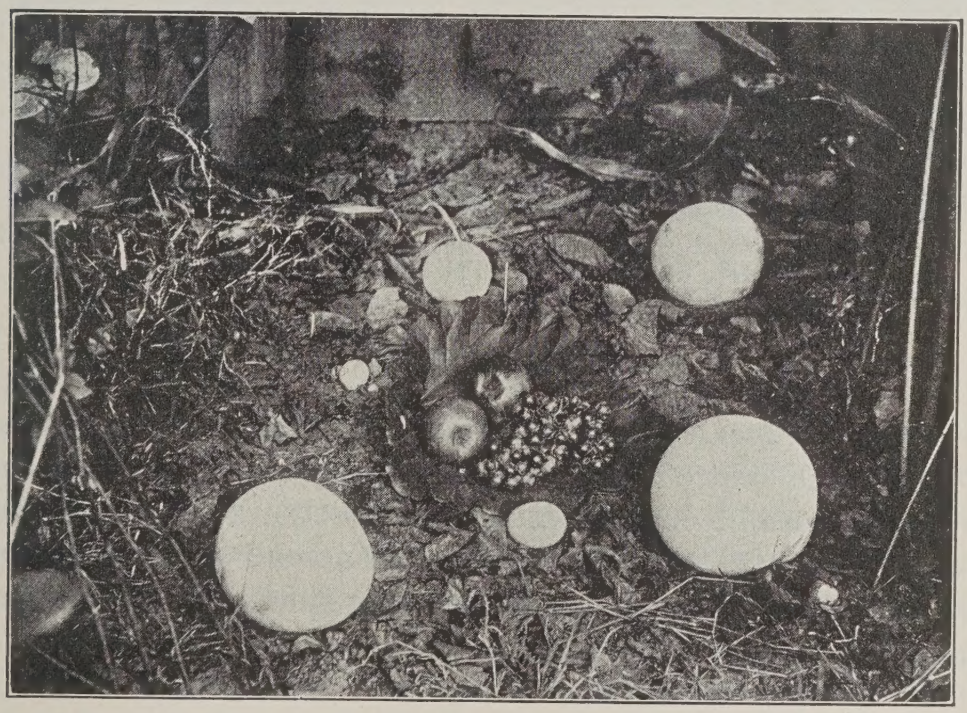


FIG. 366.—Giant puffballs (*Lycoperdon giganteum*). Note the size of the four specimens as compared with the egg and fruit in the center. (After W. A. Murrill.)

Over 14,000 species of Basidiomycetes have been described.

Life-cycle.—The life-cycle of the meadow-mushroom (Agaricus campestris) may be indicated as shown on page 511.

OTHER NON-GREEN PLANTS

In addition to the true fungi, there are two other groups of non-green thallophytes which ought to be mentioned here—one (the Myxomycetes) because of their scientific interest; the other (Bacteria) because of their economic importance.

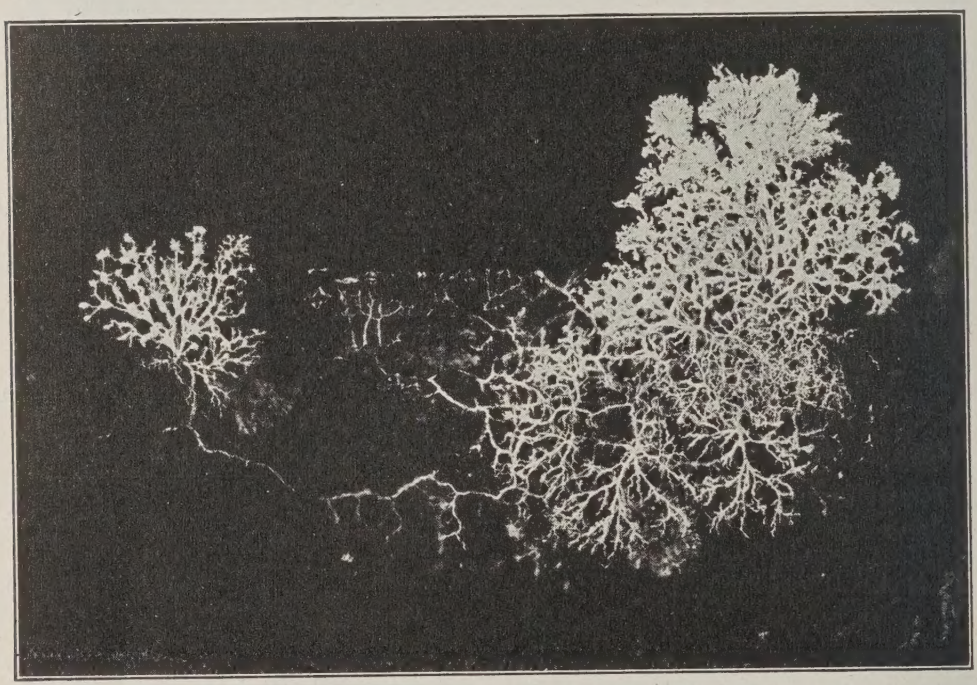


FIG. 367.—Plasmodium of a slime-mold (myxomycete), *Fuligo septica*, growing on the inner surface of a glass jar. The natural color was bright orange.

MYXOMYCETES

The Myxomycetes are on the border-line between the kingdom of plants and that of animals. In some of their characters they so closely resemble lower animals, like the *Amoeba*, that they have been claimed by the zoologists, under the name *Mycetozoa* (fungus-like animals). In their method of reproduction they are more like plants than like animals.

The details of life-history vary with different species. The body of the organism is commonly a large naked mass of protoplasm (see footnote, p. 487), called a *plasmodium*, commonly found on old decaying logs, in tan-bark, and similar places, where

moisture and organic food are abundant. The protoplasm flows over the surface on which it grows, like the *Amoeba*, taking in nourishment, at times flowing around and thus investing particles of food, assimilating, and growing in size. The protoplasm may be spread out in sheets or in a delicate network of strands, or both (Fig. 367). When viewed under the microscope the protoplasm is seen to be in almost constant motion, flowing for about a minute in one direction; gradually slowing up, it comes to rest, and then resumes its flowing, but in the opposite direction, also for about a minute. Different species possess different colors, but they never possess chlorophyll.

Reproduction.—At a certain stage of development, the plasmodium will begin to form tiny upright stalks, at the top of which will develop a sporecase, containing spores and *capillitium* (Fig. 368). The capillitium consists of hygroscopic threads which aid in the dissemination of the spores. When the spores are ripe they are scattered by the wind, and each, on germination, produces a swarm-spore. A new plasmodium results from the fusion of these swarm-spores.

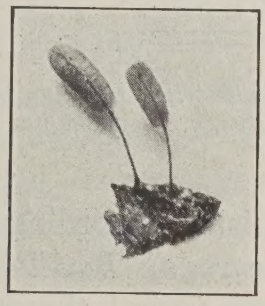


FIG. 368.—Fruiting bodies of a myxomycete (*Comatricha suksdorfii*), greatly enlarged. (Photo from type specimen.)

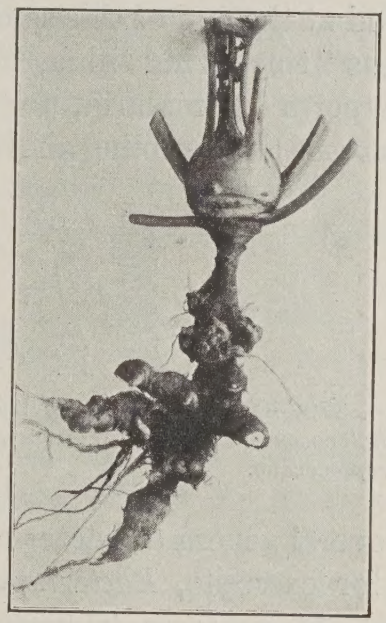


FIG. 369.—Kohlrabi, showing club-root, caused by a myxomycete, *Plasmodiophora brassicae*. (Cf. Fig. 422, *D*.)

Economic Importance.—The Myxomycetes have very little economic importance, but the disease of cabbages, kohlrabi, and turnips, known as *club-root*, is caused by a slime-mold growing on the roots (Fig. 369).

BACTERIA

The bacteria are among the very simplest plant structures known. They are one-celled, but of many shapes, and with or without motile cilia. They include the smallest living things known. There are even reasons for believing that some forms are ultra-microscopic, that is, too small to be seen with the most powerful microscopes that can be made. Some forms are less than one fifty-thousandth of an inch in diameter. Of some kinds of bacteria, as many as 300 could be placed side by side on the period at the end of this sentence. In fact the word "microbe" means "tiny living thing,"[1] though not all microbes are bacteria. The germ of malaria, for example, is a microscopic animal (*protozoon*), resembling an *Amoeba*.

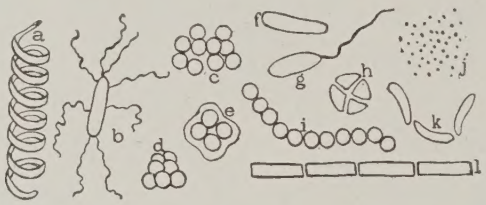


FIG. 370.—Various forms of bacteria. *a*, *Spirillum; b*, *Bacillus typhosus; c*, *Staphylococcus, d*, *e*, *j*, *h*, *Micrococcus; f*, *k*, *l*, *Bacillus; g*, *Pseudomonas pyocyanea; i*, *Streptococcus*.

Several genera of bacteria are distinguished according to shape as, for example, *Bacterium* (non-motile rods), *Bacillus* (motile rods), *Micrococcus* (spherical), *Spirillum* (spiral threads) (Fig. 370).

They are found everywhere and multiply rapidly by cell-division, whence they are called "fission-fungi" or *Schizomycetes*. Not possessing chlorophyll, they are all, of course, either parasitic or saprophytic, some being highly beneficial—in fact indispensable—to man; others highly harmful, causing some of the worst known diseases of both plants and animals. Their economic importance is briefly considered in the following chapter.

[1] From the Greek μικρός (*mikros*), small + βίος (*bios*), life.

CHAPTER XXIV

ECONOMIC IMPORTANCE OF FUNGI

In the preceding chapter we have frequently referred to ways in which our own lives are related to the life of plants. It would be difficult to say what particular group of plants affects us most, but certainly none more than the fungi. They are among the direct causes of human sorrow and happiness, of health and disease, of poverty and wealth, life and death. They are at once the foundation and the arch enemy of agriculture, the objects and obstacles of commerce, the source and hindrance of human industry.

EDIBLE FUNGI

Mushrooms and Toadstools.—Everyone is familiar with edible "mushrooms;" they are now on sale at every grocery. Nearly everyone thinks there is a difference between mushrooms and "toad-stools." Such, however, is not the case. These two terms are applied indiscriminately by the botanist to any gill-bearing fungus. The word "mushroom" is used by most people to designate the meadow-agaric (*Agaricus campestris*), which is *the* mushroom of commerce, *par excellence*. There are over 1000 fleshy fungi that are good to eat, and many more that are not poisonous, but non-edible because they are tough, or fibrous, or ill-tasting. Many of those good to eat resemble the meadow-mushroom in having a stalk and gills, and are closely related to it (Fig. 371); while others, like the "puff-balls," belong to an entirely different group. All puff-balls are good to eat when young. Many esteem the *morel* (*Morchella esculenta*) as a great delicacy.

Criterion of Edibility.—Here, as elsewhere, there is no royal road, no short cut to knowledge. There are absolutely no external characteristics which distinguish edible from poisonous fungi. The only way to tell whether a given species is poisonous

or not is to try it. Since this is so, it is best for the amateur not to make the endeavor, but to depend only upon the knowledge of an experienced mycologist. One should first seek to attain skill in determining the *exact species* of his specimen, and then follow the assurance, and especially the warnings, of some reliable book. In general, one should avoid all bright-colored species (although some of them are not poisonous), and all species that have a "cup" at the base of the stalk, or stipe. To insure no mistake in this latter point, one should always be sure that he has the base of the stipe, and has not broken it off above the base. Beginners should also avoid all specimens in the "button" stage of development, as it is very difficult to determine the exact species at that stage.

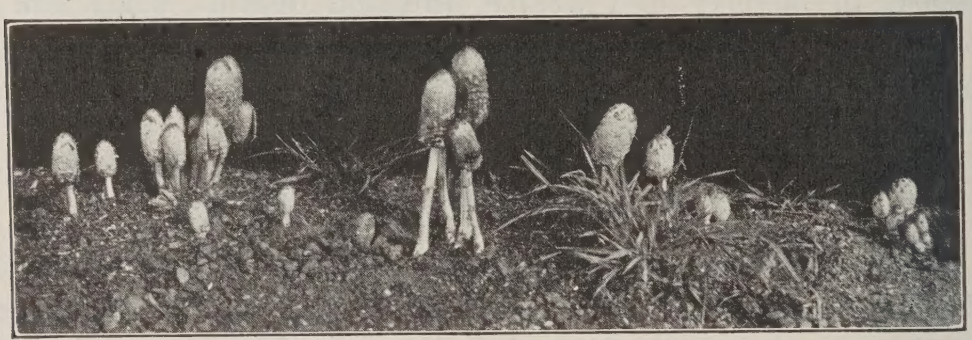


FIG. 371.—Shaggy-mane mushroom (*Coprinus comatus*). Edible before the spores turn black.

Mushroom Culture.—The growing of mushrooms for the market is a very important industry, especially in some localities. Cultures are usually started from "spawn," obtained from the seedsman in the form of "bricks," as noted on page 511. The industry is commonly carried on in cellars and caves. This is not necessary, for the meadow-mushroom, as its name clearly implies, grows in nature in open meadows and pastures. But, since the fungi have no chlorophyll, they do not need the light, and so space can be used for their culture that would not well serve any other useful purpose.

FUNGI THAT CAUSE PLANT DISEASES

Government Regulation.—Fungi that grow as parasites on green plants cause serious disturbances of the normal life-processes and structure of their hosts, interfering with healthy

growth, and causing plant diseases. Since the fungi are reproduced by spores, these diseases may rapidly spread by contagion. On this account state legislatures and the national Congress have been obliged to pass stringent laws governing international and interstate traffic in plants liable to disease, providing for their careful inspection and quarantine. The United States

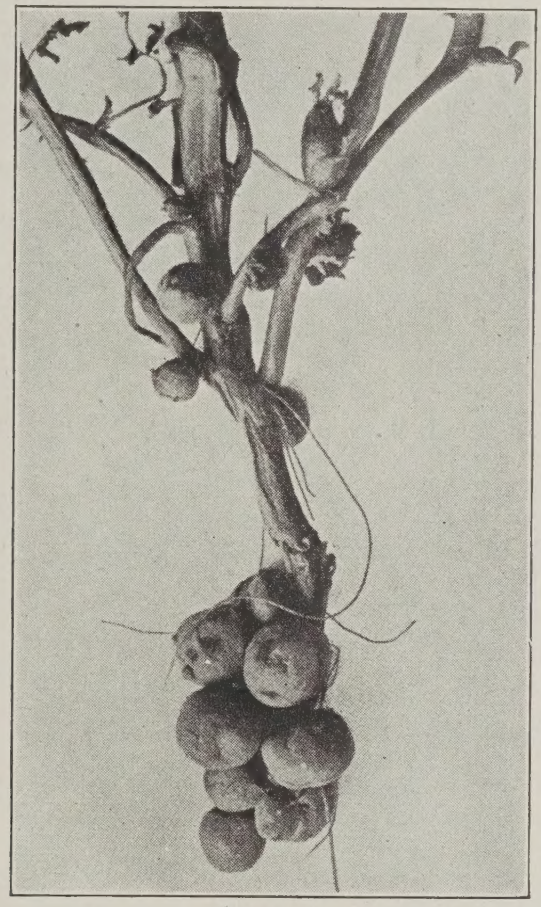


FIG. 372.—"Little potatoes," a disease of *Solanum tuberosum* caused by the parasitic fungus, *Rhizoctonia* (*Corticium vagum* var. *Solani* Burt). (After F. M. Rolfs.)

Government maintains an expert pathologist continuously at the port of New York and other ports to inspect plants imported from foreign countries. Sometimes whole cargoes of potatoes or other vegetables are refused entrance at the port, and must then be taken to sea and dumped into the ocean, or else taken to the port of some other country where the regulations are less stringent.

Diseases Caused by Phycomycetes.—Among the plant diseases caused by the alga-like fungi may be mentioned:

1. The "damping-off" disease (*Pythium de Baryanum* Hesse), which attacks young seedlings of beans and other plants near

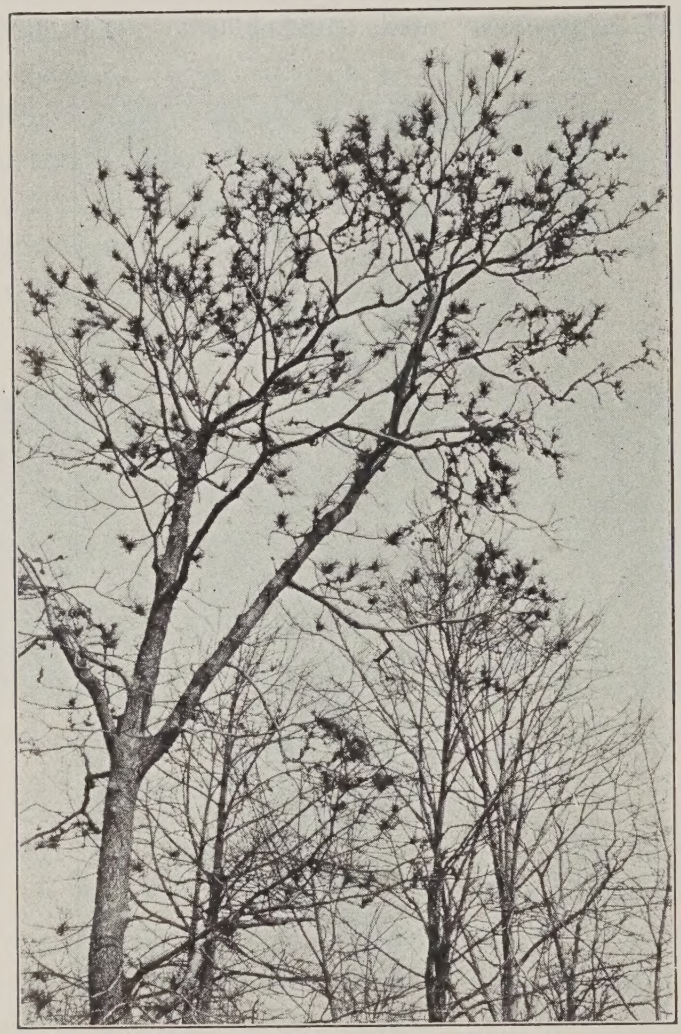


FIG. 373.—Witches' brooms on the hackberry (*Celtis occidentalis*), caused by a gall-mite (*Phytoptus*, sp.), or possibly by the mite in conjunction with a powdery mildew (*Sphaerotheca phytoptophyla*), which is usually found on the "brooms."

the surface of the ground, causing the tissues there to disintegrate, and the entire plant finally to wilt and die.

2. Brown rot of lemons, commonly seen in fruit that has been kept too long or in too damp a place.

3. "Blister-blight" or white "rust" of radishes and their relatives, such as shepherd's purse and mustard. This fungus is known as *Albugo candida*, or more recently as *Cystopus candidus*.

4. Downy mildews of grapes and cucumbers.

5. Potato rot and "late blight," *Phytophthora infestans* (Mont.) DeBary. This disease was the cause of the failure of the potato crop and the consequent famine in Ireland, in 1846–47. (The disease known as "little potatoes" (*Rhizoctonia*) and by various other names (Fig. 372), is caused by one of the *Basidiomycetes.*)

FIG. 374.—Ergot (*Claviceps purpurea*). Sclerotia on wild rye (*Elymus virginicus*), at left; on marsh grass (*Spartina sp.*), middle; on cultivated rye (*Secale cereale*), at right.

Diseases Caused by Ascomycetes.—Among diseases caused by various species of sac-fungi are the following:

1. Peach leaf-curl, plum pockets, and "witches brooms" (Fig. 373).

2. Brown rot of peach and plum. The damage caused by this disease in the state of Georgia alone, in 1900, amounted to nearly $700,000.

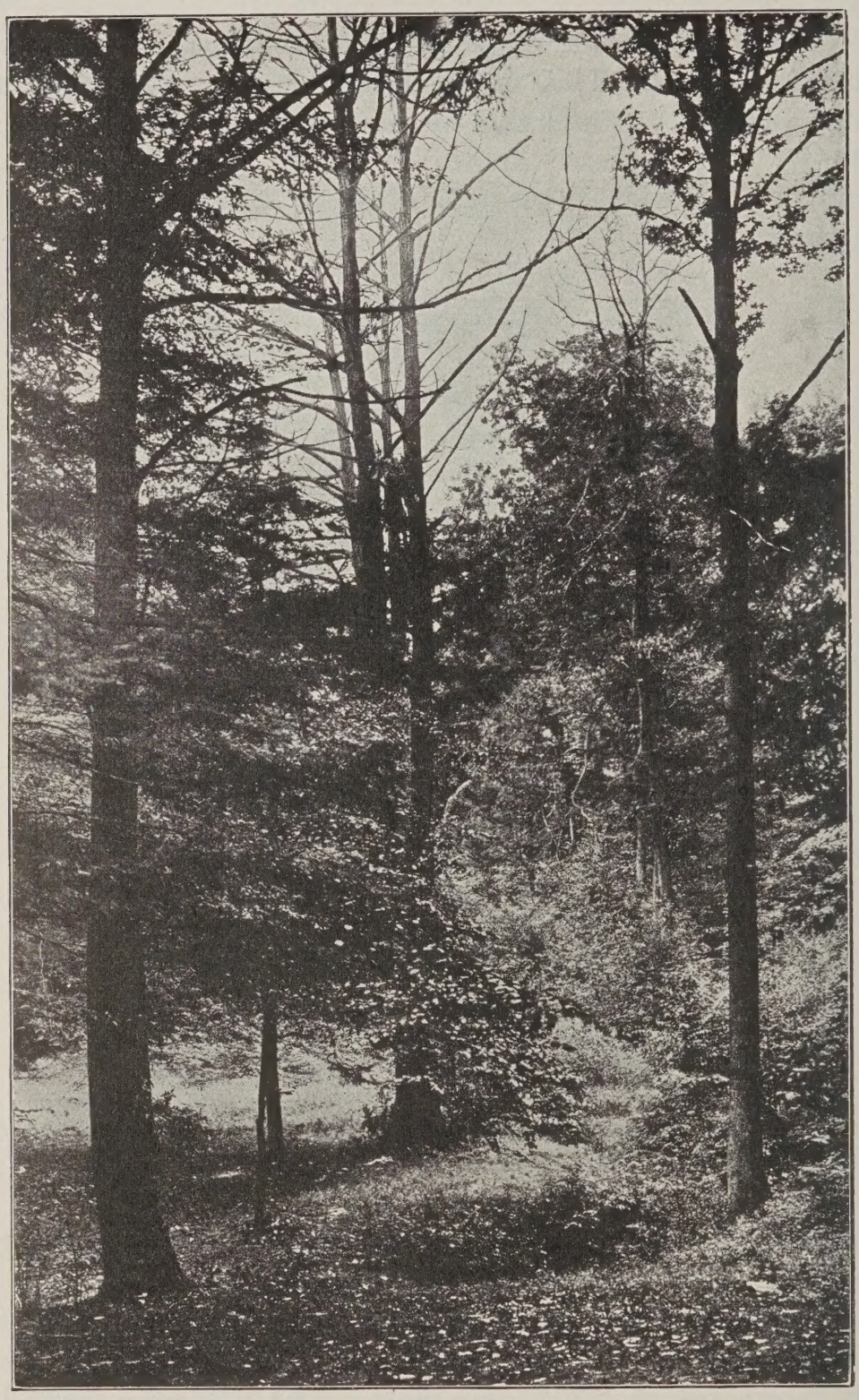


FIG. 375.—Two chestnut trees (*Castanea dentata*), killed by the destructive chestnut blight. (After W. A. Murrill.)

3. Alfalfa leaf-spot, the sooty mold of the orange, the powdery mildew of grapes and apples, the wilt disease of cotton and watermelon, the ergot of rye and other cereals (Fig. 374), the black knot of plums and cherries and the disastrous chestnut disease of the eastern United States.

4. *Chestnut Disease.*—The chestnut disease, or blight, first appeared in the vicinity of New York City about 1904, and from there as a center it has rapidly spread until it has destroyed most of the chestnut trees within a radius of over 200 miles of the city (Fig. 375). As many as 17,000 trees have been destroyed in the city of Brooklyn alone, entailing a total loss of several million dollars. The mycelium of the fungus that causes it (*Endothia parasitica*) grows underneath the bark, and for this reason it is practically impossible to check it by spraying, as the bark protects the mycelium from all known spraying solutions. The fruiting pustules of the fungus form on the surface (Figs. 376 and 377). The only method of checking the spread of the disease would be to cut down and burn all affected trees. Millions of dollars worth of damage has been caused by this disease within the past twenty years. The financial loss in New York City and vicinity, alone, has been estimated at much more than $5,000,000, while the loss for the entire United States, up to 1911, was estimated by the Federal Government at not less than $25,000,000. In 1910, the State of Pennsylvania appointed a special commission of experts for the investigation and control of the disease, and appropriated over $275,000 to meet the necessary expense of the work.

FIG. 376.—Chestnut blight. Portion of a branch of an American chestnut (*Castanea dentata*), which had been artificially inoculated with the spores of the chestnut-blight fungus, *Endothia parasitica* (Murr.) Anders. The white areas are infected spots. (After W. A. Murrill.)

Smuts.—The important Grain Smuts have already been discussed in the preceeding chapter.

Rusts.—The life history of the wheat rust (*Puccinia graminis*) was outlined in Chapter XIX. This fungus has not only caused millions of dollars worth of damage to the wheat crop of the world but has been the cause of legislative enactments. As early as 1760 there was passed in Massachusetts "An Act to prevent

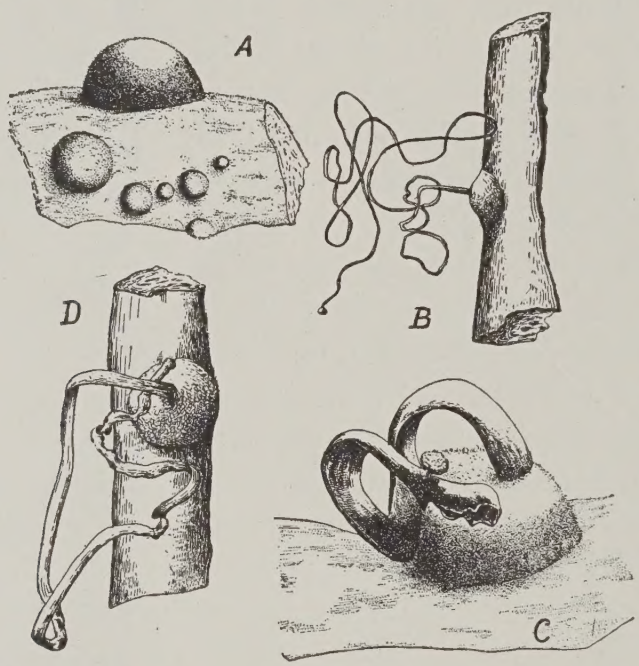


FIG. 377.—Chestnut-blight fungus (*Endothia parasitica*). Fruiting pustules and spore-masses from cultures. × about 8. *A*, stages in the development of the pustules; *B*, *C*, *D*, various forms of spore discharge in a moist atmosphere. (After Murrill.)

Damage to English Grain arising from Barberry Bushes." This act read, in parts, as follows:

"Whereas it has been found by experience, that the Blasting of Wheat and other English Grain is often occasioned by Barberry Bushes, to the great loss and damage of the inhabitants of this province:

"Be it therefore enacted by the Governour, Council, and House of Representatives, that whoever, whether community or private person, hath any Barberry Bushes standing or growing in his or their Land, within any of the Towns in this Province, he or they shall cause the same to be extirpated or destroyed on or before the thirteenth Day of June, Anno Domini One Thousand Seven Hundred and Sixty.

"Be it further enacted that if there shall be any Barberry Bushes standing or growing in any land within this Province, after the said 10th day of June, it shall be lawful, by Virtue of this Act, for any Person whosoever to

enter the Lands wherein such Barberry Bushes are, first giving one month's notice of his intention to do so to the Owner or Occupant thereof, and to cut them down, or pull them up by the root, and then to present a fair account of his labour and charge therein to the owner or occupant of the said land; and if such owner or occupant shall neglect or refuse by the space of two months next after the presenting said account, to make to such person reasonable payment as aforesaid, then the person who cut down or pulled up such bushes, may bring the action against such owner or occupant, owners or occupants, before any Justice of the Peace, if under forty shillings, or otherwise before the Inferior Court of Common Pleas in the County where such Bushes grew, who upon proof of the cutting down or pulling up of such bushes by the person who brings the action, or such as were employed by him, shall and is hereby respectively empowered to enter up judgment for him to recover double the value of the reasonable expense and labor in such service and award execution accordingly.

"Be it further enacted, that the Surveyors of the Highways, whether public or private, be and hereby are empowered and required *ex officio* to destroy and extirpate all such Barberry Bushes as are or shall be in the Highways in their respective Wards or Districts, and if any such shall remain after the aforesaid tenth Day of June, Anno Dominio One Thousand Seven Hundred and Sixty, that then the Town or District in which such bushes are shall pay a Fine of two shillings for every bush standing or growing in such Highway, to be recovered by Bill Plaint, Information, or on the Presentment of a Grand Jury, and to be paid one Half to the Informer and the other Half to the Treasury of the County in which such bushes grew for the use of the County."

In England, Scotland, Denmark, Scandanavia and Central Europe there is little black-stem-rust because the barberry bushes have been systematically eradicated. In some of these countries (Denmark, Norway, France, Germany, Austria, Hungary, Canada, the United States, and others) there are laws compelling the destruction of barberry. But in the Alps, where barberry bushes are common the fields of rye are black with rust.[1]

The rate at which barberry bushes may spread by seeding is strikingly illustrated by two cases reported by Kempton.[2] A farmer in Wisconsin planted a few bushes as a hedge near his house. Cattle browsed on the bushes and ate the fruit. In this way the seeds were distributed over an adjoining wooded pasture of 300 acres. In thirty years the number of bushes derived from

[1] Stakman, E. C. Barberry eradication prevents black rust in western Europe. U. S. Dept. Agr. Dept. Cir. 269. April, 1923.

[2] Kempton, F. E. Progress of barberry eradication. U. S. D. A. Dept. Cir. 188. Washington, Oct., 1921.

seeds of the original hedge was estimated at 35,000. In Champaign County, Ohio, two farms were found in 1920 having numerous barberry bushes extending over an area having a radius of

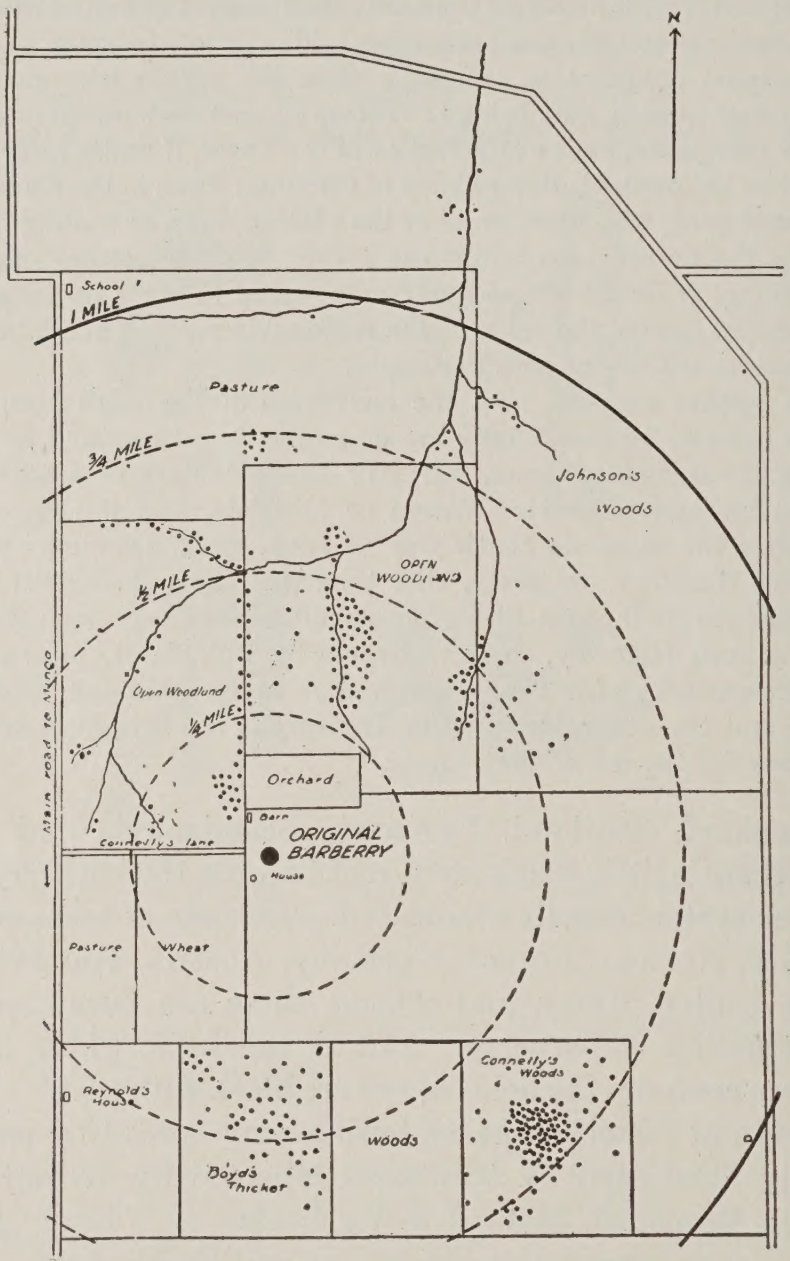


FIG. 378.—Map showing large numbers of escaped barberries (small dots) developed from seed scattered by birds, from a single original bush (large dot) on a farm near Mingo, Ohio. (After Kempton, U. S. Dept. Agr.)

more than one mile. These bushes had originated from a single bush planted near one of the farmhouses more than 100 years previously (Fig. 378).

In South Dakota there was found a hedge of 50 barberry bushes more than 15 years old, together with about 25 seedlings nearby. All wheat and wild barley within 200 feet of the barberries was found to be infected. The grain was infected for as

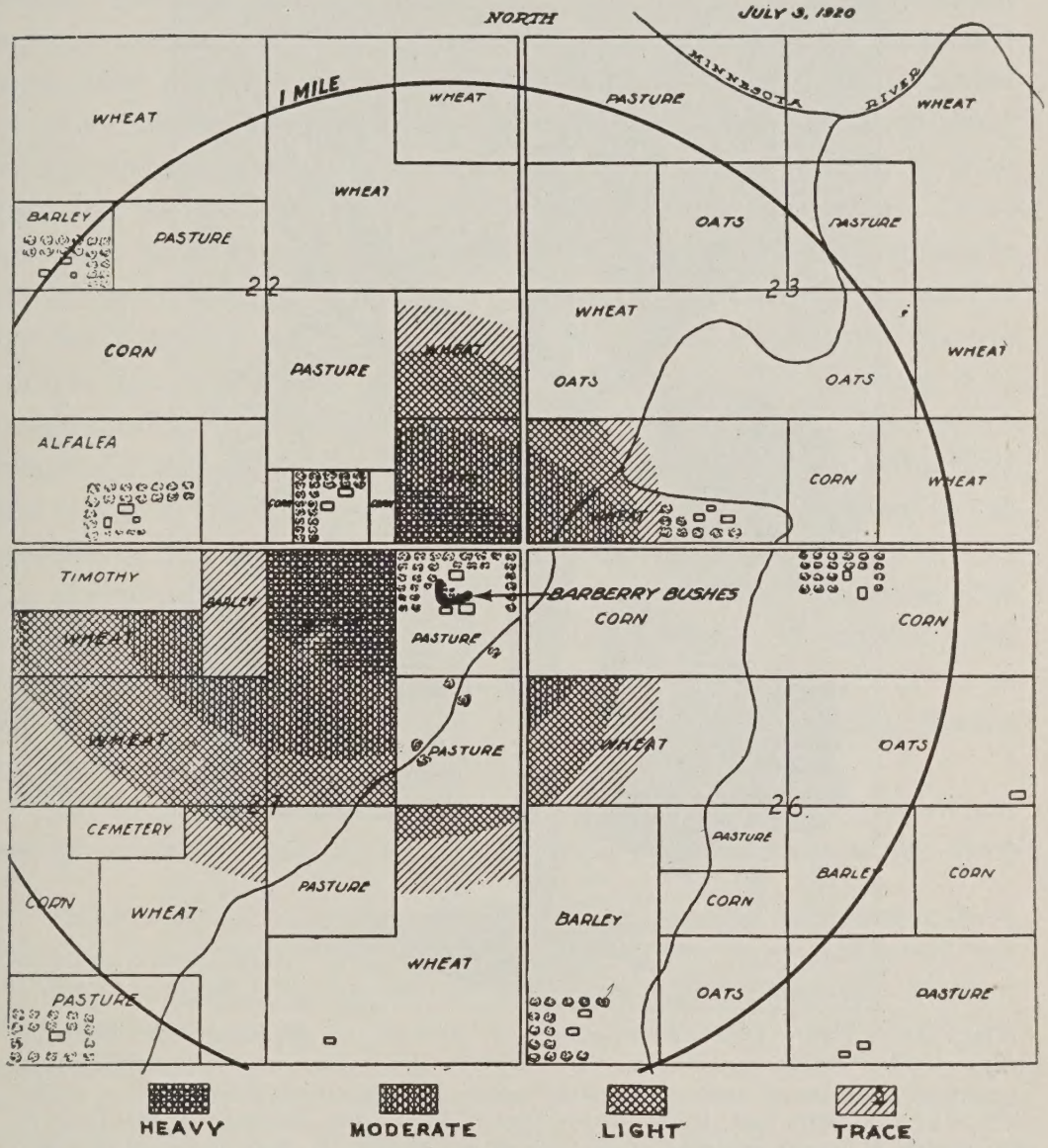


FIG. 379.—Map showing the spread of black stem-rust from a hedge of common barberry in Sisseton Township, South Dakota in 1919. The density of the shading is in proportion to the severity of rust infection on grains and grasses in the surrounding fields. (After Kempton, U. S. Dept. Agr.)

much as a mile from the barberries, the amount of rust diminishing noticeably as the distance from the hedge increased (Fig. 379).

In addition to the rust of wheat, there are also rusts of the carnation and the clover caused by species of *Uromyces*. The

carnation rust, which first appeared about 1892, is common in the plant houses of commercial florists.

White Pine Blister-rust.—Among the more important plant diseases recently appearing in the United States is the White

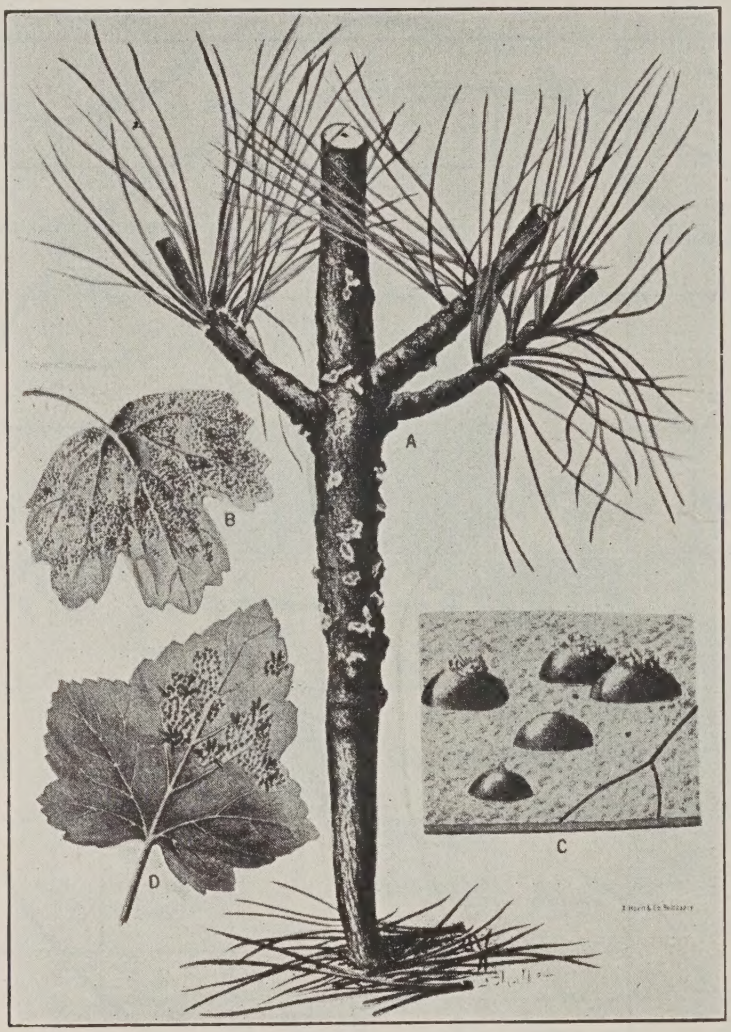


FIG. 380.—White Pine blister-rust. *A*, portion of diseased tree, showing aecial blisters broken open; from these blisters the spores spread to neighboring currant or gooseberry bushes; *B*, early summer stage (urediniospores) on under surface of a currant leaf; these spores repeat during the summer, at intervals of two weeks; *C*, early summer stage, much magnified; *D*, late summer and fall (teliospore) stage, on the under surface of a currant leaf; from this stage the disease spreads again (by basidiospores) to pine trees. (After Perley Spaulding, by courtesy of the U. S. Dept. of Agriculture.)

Pine Blister-rust, introduced from Europe about 1909. There is a large number of different rusts that attack pines, but the disease commonly referred to as the White Pine Blister-rust is caused by the fungus, *Cronartium ribicola,* which passes its aecial stage on

five-leaved pines, where it is commonly known as *Peridermium Strobi*(from the specific name of the white pine—*Pinus Strobus*). This rust attacks only pines that have five leaves to the fascicle.[1]

The telial stage, as its name indicates, is passed on species of *Ribes* (currants and gooseberries[2]) (Fig. 380). The blister-rust spores produced on the white pine cannot infect other pines nor any other plants except currants and gooseberries. The spread of the disease, therefore can be controlled only by destroying every currant and gooseberry bush growing near enough to pine trees to be infected with the aeciospores from the latter. But *how near* to pines may the *Ribes* safely be grown? It is certainly a matter of miles, for the spores remain viable after being carried by the wind for many miles. Spaulding and Rathbun-Gravatt[3] found that teliospores may remain viable for 19–87 days, and uredospores for as long as 59 days, varying with external conditions and with the species. Gravatt and Posey[4] have found that the larvae of the Gipsy-moth are active agents in the spread of the disease. The larvae on pines work among the rust blisters and the spores adhere to their hairy bodies in such large numbers that their bodies appear to be the color of the spores. It has also been found by Collins[5] that gipsy-moth larvae may be blown as far as 20 miles by the wind. White pines and *Ribes*, therefore, should be grown more than 20 miles apart.

The importance of such a disease as this may be inferred when we consider that the value of the white pine growing in the New

[1] Another pine tree blister-rust which attacks species of pine that have less than five leaves to the fascicle, such as *P. contorta*, *P. ponderosa*, and *P. rigida*, is caused by *Cronartium pyriforme*, which is the telial stage of *Peridermium pyriforme*. The aecial stage (*Peridermium*) appears on the pine, while the alternating host is the False Toad-flax (*Comandra umbellata* and *C. pallida*). The *Comandra* is itself a parasite on the roots of various species of blueberry (*Vaccinium*) and other woody plants.

[2] By some systematists the gooseberries are placed in a separate genus, *Grossularia*.

[3] Spalding, P., and Annie Rathbun-Gravatt. Jour. Agr. Res. **31**: 901–916. Nov. 15, 1925.

[4] Gravatt, G. F. & G. B. Posey. Gipsy-moth larvae as agents in the dissemination of the white-pine blister-rust. Jour. Agr. Res. **12**: 459–462. Feb. 18, 1918.

[5] Collins, C. W. Dispersion of gipsy-moth larvae by the wind. U. S. Dept. Agr. Bull. No. 273. 1915.

England states is estaimated at $75,000,000, that of the Lake states, at $96,000,000, of the Western states at $60,000,000, and of other National forests at $30,000,000, a total of $261,000,000. The western sugar pine (*Pinus Lambertiana*), one of the five-leaved pines, has a total value estimated at $150,000,000. Thus, timber to the value of $411,000,000 is threatened with destruction by this one parasitic disease (*Cf.* Figs. 381 and 382).

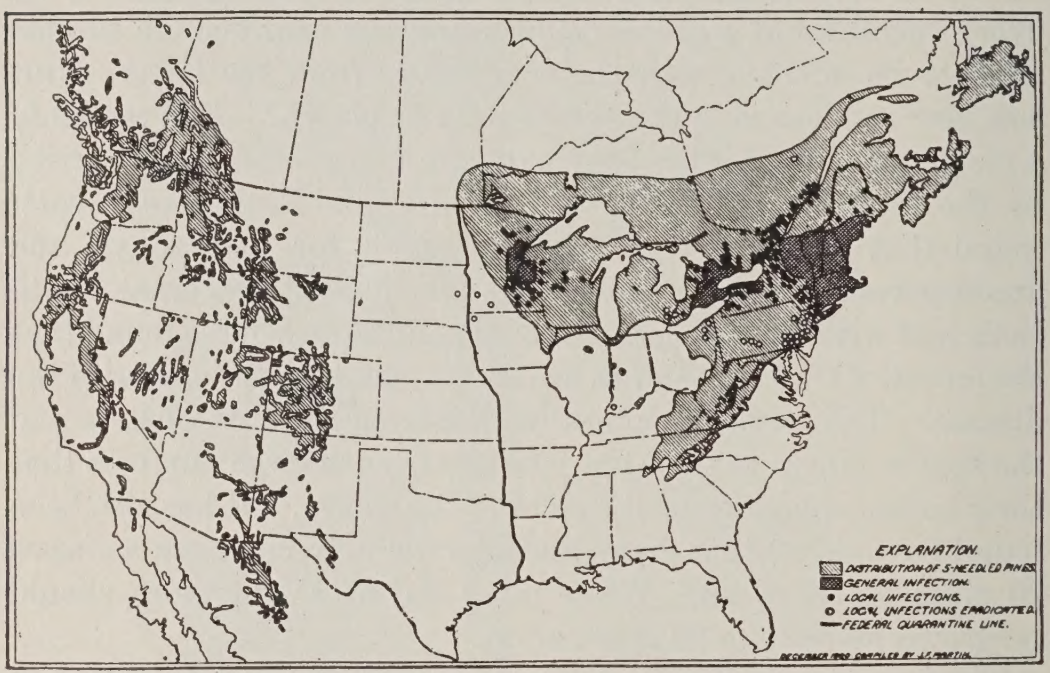


FIG. 381.—Outline map of the United States and adjoining portions of Canada and Mexico, showing the distribution of the 5-needled pines of North America and the white pine blister-rust. The disease is not present west of the Federal quarantine line extending along the western boundaries of Minnesota and Louisiana and the States between. The shipment of 5-needled pines and gooseberry plants into the Western States from points east of the quarantine is prohibited. (After Martin. U. S. D. A. Dept. Cir. 177. 1921.)

"The greatest protection to currant and gooseberry growers, as well as pine owners, is afforded by the general destruction of cultivated European black-currant plants[1] throughout the country. The blister rust . . . has not yet (1924) spread into many States and localities. It is important to keep the disease out of disease-free regions as long as possible and to delay its progress in regions where it has begun its ravages. To accomplish this, the destruction of cultivated black currants in all States where white

[1] *Ribes nigrum* L.

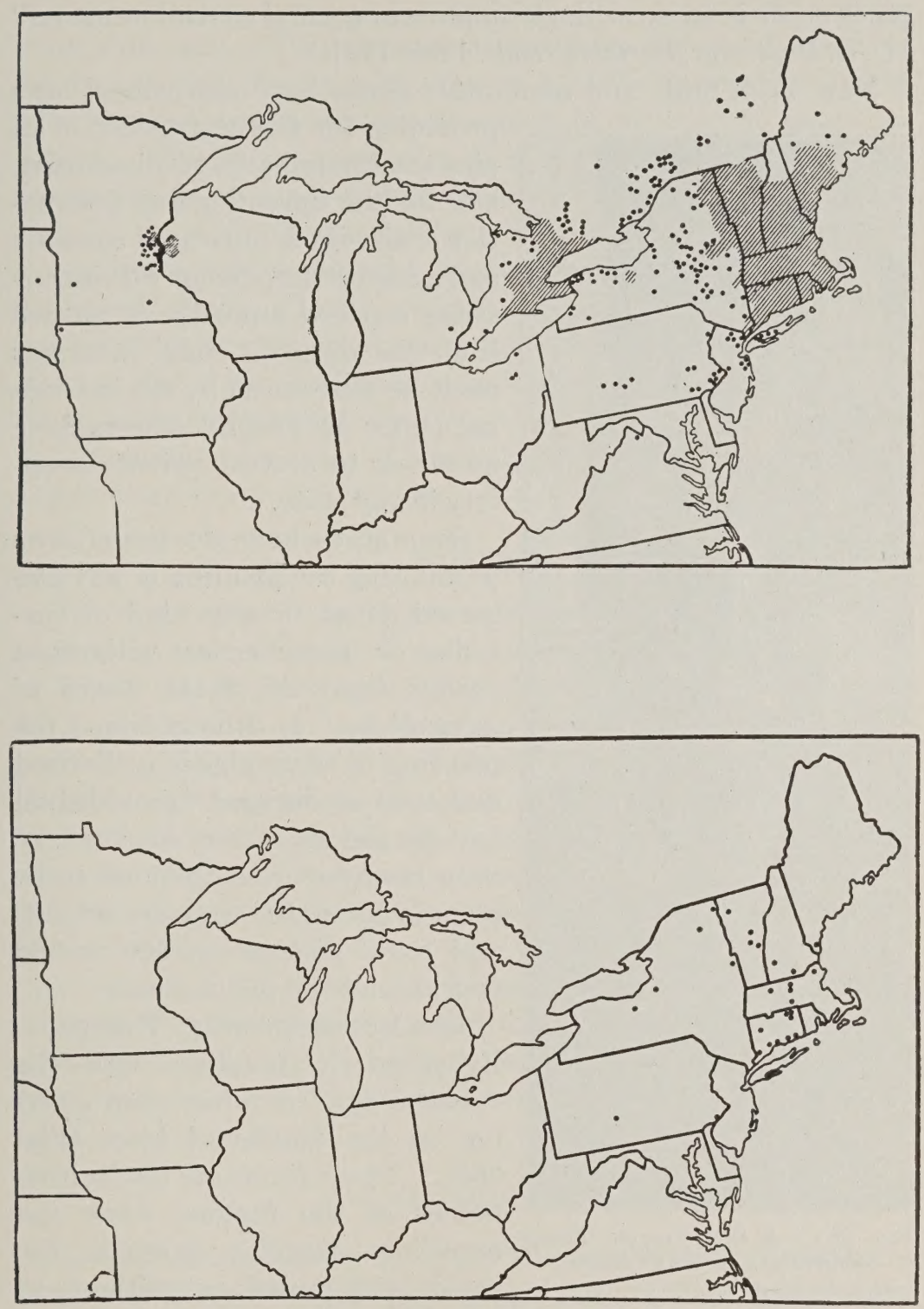


FIG. 382.—Outline maps of the United States showing the known distribution of white pine blister-rust in North America to and including 1909 (lower map black dots), and to and including 1917 (upper map, black dots and cross hatching). (After Perley Spalding. U. S. D. A. Bull. 957. 1922.)

pines occur is an exceedingly important general control measure." (*U. S. Dept. Agr. Farmers' Bull.* 1398, 1924.)

New York State and some other states have also passed laws providing for the destruction of all pine trees found to have blister-rust, and for the uprooting and destruction of all wild or cultivated currants and gooseberries, except within nurseries certified annually to be free from the disease. Such measures must be authorized by the individual states as Federal officers have no power to destroy private property in any state.

FIG. 383.—A shelf-fungus (*Fomes applanatus*) on sugar maple.

Some states have also passed laws prohibiting the planting of any five leaved pines or any kind of currants or gooseberries without a permit from the State Board of Agriculture. In Rhode Island the planting of white pine is authorized and even encouraged "provided all currant and gooseberry bushes have been removed from the area to be planted before the trees are set out, and for a distance of 600 to 900 feet around the planted area."

Timber-destroying Fungi.—Everyone is familiar with the "shelf-fungi," so often seen growing on the trunks of trees (Fig. 383). These forms are the fruiting bodies of the fungus, while the mycelium ramifies through the wood, often in such quantities as to form the "punk," formerly much used in setting off fireworks. The soft fungal threads are enabled to make their way through the hard woody tissue by means of an enzyme which they secrete. The enzyme softens and dissolves the cell-walls

of the wood, thus making it possible for the mycelium to penetrate with ease. This process disintegrates the wood, weakens the tree so that it eventually dies or is easily blown over by the wind, and of course renders the wood of little or no value for timber. The fungus gains admission to the tree by means of the spores falling on some surface freshly exposed by trimming the tree, by the accidental breaking of branches, by the "barking" caused by lawnmowers, and in other ways; on account of the disastrous results, all such surfaces should be protected by being painted over as soon as a branch is cut or broken off, or a portion of bark removed. There are many species of wood-destroying fungi, and the financial loss they cause to the lumber industry, not to mention the losses of beautiful shade trees in lawns, parks, and streets, is very considerable.

MOLDS

The filamentous fungi, commonly known as molds, belong to various species. The black mold (*Rhizopus nigricans*)[1] common on bread, and the blue mold (*Penicillium*) (Fig. 340) on decaying fruit and on fruit canned at home, have been described in the preceding chapter. The appearance of the mold indicates that the fruit was not sufficiently sterilized before the jar was sealed. In fact, the entire process of canning is a series of operations intended primarily to kill all germs of bacteria and fungi. The sterilized fruit is then sealed from the air and from access of other germs while it is still hot. The "keeping" of canned goods depends upon the successful exclusion of *every* living spore or other germ. If goods preserved in tin cans have been imperfectly sterilized the gases produced by fermentation will exert a pressure upon the can from the inside, often strong enough to cause a bulging of the ends.

COLD STORAGE

Just as canning has for its object the preservation of vegetable or animal tissues by killing the germs with heat, so cold storage accomplishes the same end by means of extreme cold. Most

[1] Linnaeus called this mold *Mucor Mucedo* in his "Species Plantarum" (1753). It is often designated in modern literature as *Mucor stolonifer* Ehrenberg (1818) and *Rhizopus nigricans* Ehrenberg (1820).

germs remain inactive below a certain temperature, which may be readily ascertained by experiment. The spoiling of eggs is caused by the presence within the egg of a germ- "flora," which lives upon the yolk and white, producing by its life processes, the noxious gases of stale eggs. At certain low temperatures most of the life-processes of the germs are either stopped entirely, or greatly retarded.[1] In the colonial days of America, and later, it was common for dwellers on farms and in villages to preserve meat by burying a quantity of it in the snow during the winter season—a primitive cold storage. During cold storage, however, certain chemical changes (auto-digestion or *autolysis*) slowly take place in the preserved tissue, due to enzyme action. As a result there is a limit to the period that food can be kept in cold storage without deteriorating. All cold-storage plants and refrigerator cars are evidence of the fact that our own lives are profoundly affected by the existence and activity of microscopic forms of plant life.

BACTERIA

Extent of Their Influence.—The study of bacteria, the smallest of all known plants, has become so extensive as to form a separate science, bacteriology; and it will not be possible here to more than suggest in outline the numerous important ways in which these tiny plants affect our daily lives. In fact their discovery has practically revolutionized our method of living in many ways. Modern methods of sanitation and hygiene, public and private, modern house furnishing, as, for example, the substitution of bare floors with rugs in place of carpets, modern views of disease and methods of treating it, and the technique of innumerable industries, both agricultural and manufacturing, have all been profoundly modified or determined altogether by the discovery of bacteria, and the extension of our knowledge concerning them.

[1] When fresh eggs are packed in salt or in water-glass (sodium or potassium silicate) fresh air is prevented from diffusing through the porous shell. By this means partial or complete anaerobic conditions result within the shell, thus retarding or preventing the growth and multiplication of aerobic bacteria that would otherwise cause the eggs to spoil.

Bacteria and Plant Diseases.—In addition to the plant diseases caused by fungi, as previously mentioned, a number are known to be caused by bacteria. The "wilt" of sweet corn, a disease first discovered on Long Island, is caused by bacteria, as is also the *crown gall*, a tumorous or cancerous-like disease common in the rose family (peaches, apples, roses, raspberries),

FIG. 384.—Louis Pasteur, founder of the science of bacteriology.

and the willow, grape, and walnut (Fig. 385). The bean blight and pear blight, the soft rot of the calla-lily, and the "wilt" of cucumbers and melons, are also caused each by its own peculiar kind of bacteria. On account of their nature these diseases may all be transmitted from one plant to another of the same kind.

The first known bacterial disease of plants ("fire blight" of pears—*Bacillus amylovorus*) was discovered and experimentally

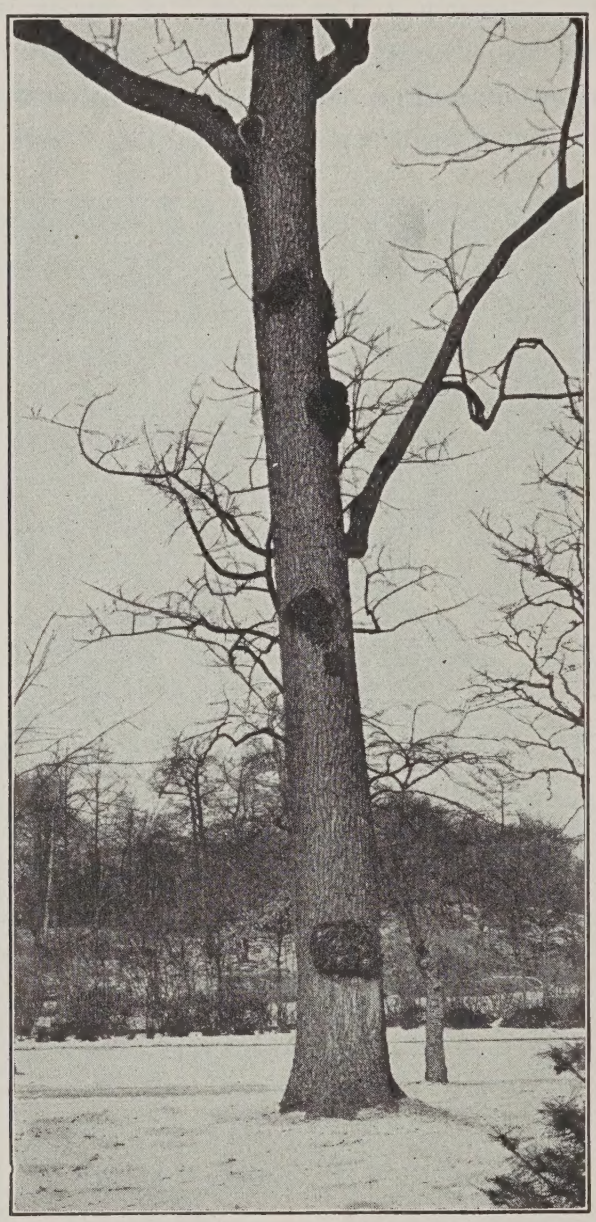


FIG. 385.—Tumors on a black walnut (*Juglans nigra*); probably crown galls caused by bacteria.

demonstrated in 1878 by Professor Burrill,[1] at the University of Illinois.

[1] THOMAS JONATHAN BURRILL. *b.* Pittsfield, Mass., April 25, 1839; *d.* Urbana, Ill., April 14, 1916. For 44 years professor at the University of Illinois (1868–1912). By the Forestry Park, on the campus of the University of Illinois, he demonstrated for the first time that trees could be successfully grown on the North American prairie.

Contagious and Infectious Diseases.—The ease with which such tiny organisms as bacteria can be transferred from one place to another makes the diseases they cause easily transmissible or "catching." We actually do "catch cold;" that is, our all too common "colds" are due to the presence of "cold-" producing germs. Arctic explorers testify to the fact that notwithstanding the great exposures to which they are subjected, they never "catch cold." This is explained by the absence of the "cold" germs that cause colds in other climates or regions.

When the members of the Peary arctic expedition of 1908–09 were in the field away from the heat and infective dust of the ship they were practically immune from colds and respiratory troubles. "The fact that colds are due to bacteria was clearly demonstrated in the Arctic. We might be precipitated into icy water with the air many degrees below zero; our clothing saturated with moisture on the march; yet we could sleep in our damp garments without fear of taking cold."[1]

Immunity.—This is not the place to discuss the various theories of immunity, but the fact should be noted in passing. It is a common belief that one who has had a contagious disease such as measles, the mumps, or whooping cough, cannot have the same disease again. While this is extremely doubtful, it is known that once having a disease does render one less liable to contract it a second time. When the germs multiply in the body with the first attack, the toxin they produce stimulates the various cells to secrete an *antitoxin*, which counteracts the toxin, or poison. Thus the patient not only "gets well" but is rendered immune for a longer or shorter period of time. Some persons appear to be naturally immune to certain diseases (*e.g.*, hay fever), while others are specially susceptible.

Disease Carriers.—Persons who are immune may, however, unknowingly transmit the disease-germ from one person to another. They are called "carriers." Typhoid fever, caused by *Bacillus typhosus*, is often transmitted by "typhoid carriers," a well-known case being that of "Typhoid Mary," a domestic servant near New York City, who for several years endangered the lives of others in homes and hospitals where she was employed.

[1] From a letter to the author from John W. Goodshell, M. D., Surgeon of the Peary arctic expedition of 1908–09.

The menace of such persons to public health justifies their permanent isolation.

Combating Disease.—There are two ways of combating disease in either plants or animals: (1) to guard against it in advance (*prophylaxis*), thereby endeavoring to prevent its appearance; (2) to treat it after it has appeared. Obviously the former is the more important and effective. The most effective prophylactic measures are the following:

1. *Personal hygiene*, involving bodily cleanliness, temperate habits, and careful diet. With plant diseases hygienic measures include such practices as sterilizing seeds before planting, by rinsing them in solutions of some germ-killing substance, like formaldehyde; spraying or dusting plants with *fungicides* (fungus-killing substances); washing the branches and foliage with various solutions, such as whale-oil soap (good for scale insects); painting the cut surfaces of trees, after pruning, to prevent the mycelium of germinating fungus spores from entering the woody tissue, and insuring good irrigation, nutrition, and cultivation.

2. *Public hygiene, or sanitation*, which means maintaining healthful surroundings. In the case of animal diseases this includes preserving a pure public water supply, proper sewage systems, clean streets, a pure milk supply (especially a healthful condition of the cows and their surroundings), and a careful inspection of meat and all other foods shipped and sold in public.

In the case of plants, sanitation includes preserving a proper drainage and aeration of the soil; maintaining a pure atmosphere, and especially one free from smoke and the poisonous gases that accompany it; fumigating in plant houses with potassium cyanide fumes, or with tobacco smoke to kill scale insects and other insects, the burning up of trees or other plants infected with a transmissible disease, such for example, as the chestnut bark disease, or barberry bushes carrying wheat rust, and eradication of injurious fungi from the soil of cultivated fields by crop-rotation, as indicated in Chapter VII.

3. *Quarantine.*—In earlier times, when a ship approaching a foreign shore was suspected of having any contagious disease on board (in particular the plague), it was prohibited by law from approaching the shore and landing its passengers or goods for a period of 40 days. The French word for forty is *quarante* (from

the Latin *quadraginta*), hence the term, *quarantine*, which now refers to any prohibition by law of intercourse, travel, shipment of goods, landing of cargoes, etc., for the purpose of preventing the spread of any communicable disease. When one member of a family is sick with a contagion, he should be confined to one room or portion of a house and not allowed to mingle with other persons until he is pronounced well, and his clothes and apartments have been thoroughly disinfected. Hospitals have "isolation wards" or even separate buildings where patients with contagious diseases are kept away from other patients. Immigrants coming to America are placed "in quarantine" and carefully examined for such diseases before they are allowed to land. If they have a contagious disease they are kept in quarantine, *i.e.*, isolated, until they are well; in some cases they may be compelled to return to their native land.

4. *Vaccination.*—In 1796 the physician Jenner observed that persons who had cowpox, a mild form of smallpox, were commonly immune to the latter. Reasoning from this he developed the method of *vaccination*. By this method the cowpox is first given to a calf or a heifer, or sometimes to an adult cow. At the end of five to seven days pustules occur on the infected surface of the animal. A watery substance that exudes from these pustules is then collected by sterile instruments and carefully tested to make sure that it does not contain any germs of tuberculosis or other disease. This substance is the *vaccine*, and in vaccination a small portion of it is applied to a scratched or slightly lacerated area on a person's arm. A mild form of the disease results, causing the formation of an antitoxin in the person's blood, and thus rendering him *actively immune*. The word vaccination is derived from the Latin word *vacca* (a cow), in allusion to the method of obtaining the vaccine. It has been calculated that, in large armies, fully as many lives have been saved from disease by vaccination against typhoid, cholera, and other diseases as are lost in battle.[1]

[1] Long before Jenner, immunity to smallpox was obtained by the practice of "ingrafting" or *inoculation* with material obtained from the pustules of those who were suffering from a mild form of the disease. In China, in the latter part of the Ming dynasty, inoculation was accomplished by blowing this secretion (containing, of course, the germs of the disease) into the nostrils.

5. *Serum-therapy.*—The treatment of germ diseases by serum-therapy consists in injecting into the blood of the patient an antitoxin, specific for the disease to be treated. The antitoxin is contained in the blood-serum of some animal that has had the given disease. As in the case of the preparation of vaccine, the animal is first placed in quarantine, under the most perfect sanitary surroundings; if found free from all contagious diseases, and otherwise satisfactory, he is given increasingly large doses of the toxin or the virus that causes the given malady. This treatment may require as long as six weeks, and results in the formation of quantities of the antitoxin in the blood. A quantity of blood is then drawn from the animal, and the blood-serum isolated, filtered, carefully tested for purity, content of antitoxin, and freedom from disease-germs, and finally put up in glass syringe containers ready for use. When a person is exposed to the given disease (*e.g.*, diphtheria), or has actually contracted it, the serum is injected into his circulatory system, where the antitoxin counteracts the toxin of the disease. The patient is thus rendered *passively*[1] *immune.* Serum-therapy (not applicable) is now successfully employed in the treatment of diphtheria, tetanus (lockjaw), hog cholera, and, with more or less success, of infantile paralysis and certain other diseases.

6. *Antiseptic Surgery.*—The greatest obstacle to successful surgery has always been the presence of the rich and varied microscopic flora, or plant life, in the air. When a wound was opened or a cut made the germs composing this flora found on the cut surface the most favorable conditions for their growth and multiplication, and the poisons they secreted interfered with the healing of the wound and caused gangrene, or inflammations, often more serious than the disease for which the operation was

---

Inoculation was introduced into England by Lady Mary Wortley Montagu, who found the practice common in Constantinople about 1717. The practice encountered both medical and religious prejudice in England. It is of interest to note here that the secretion to be used was, in Turkey, preserved and transported in nut shells. This container was doubtless effective because the interior of an unopened and perfectly sound nut would (to use modern terminology) be perfectly aseptic. Lady Mary Wortley does not mention what kind of nut was used. Montagu. *Works*, etc. London, 1803, **1**: 35; **2**: 217; **3**: 127.

[1] Passively, because the antitoxin is not produced by the activity of his own cells, as it is in the case of vaccination.

undertaken. When the discovery of bacteria, and of their universal presence, enabled men to understand these facts, it was only a step to the practice of making the operating rooms, the surgical instruments, the hands of the surgeon and attendants, and the surface to be cut, *absolutely* aseptic or sterile, thus making possible the almost unbelievable achievements of modern *antiseptic surgery*. Only a step! But what a wonderful and all-important step for the human mind to take. The honor and credit for taking it belong chiefly to the famous English surgeon, Lord Lister.

Combating Plant Diseases.—The term "plant diseases" is commonly used in a broad sense to designate almost any condition or cause of ill health in plants, including physiological disturbances (such as poor development of chlorophyll, arising from whatever cause), bacterial infection (as in "fire blight" of pears), and troubles caused by the innumerable insect and fungus pests of plants. Strictly speaking it is better to confine the term disease to the unhealthy condition of the plant, and refer to the causal agents as the *pathogenes*, or disease-causers.

Treatment for plant diseases is confined largely to applying insecticides and fungicides (by spraying, dusting, or otherwise), or to removing the pathogenes by washing the leaves and other parts with suitable solutions, or even by mechanically removing them as in the probing for borers in woody plants. Successful methods of treatment can be determined only in the light of an accurate knowledge of the life history of the organism that causes the disease. But the combating of plant diseases by the treatment of sick individuals becomes ineffective or impossible in such cases, for example, as the infection of acres of wheat with smut or rust. In such cases the diseases are best combated either by prophylaxis or by breeding disease-resistant varieties, which is, in effect, a prophylactic measure.

Prophylactic methods include proper fertilizing and cultivation to insure vigorous plants; proper treatment of the soil before planting; immersing the seed in hot water (which has been found effective, for example, for Loose Smut of wheat, and Naked Smut of barley); sprinkling the seed with a weak solution of formalin (which may largely or entirely prevent Loose Smut of oats); dipping the seed in a solution of copper sulphate (blue-stone)

(effective with Bunt of wheat); exercising care not to pass clean or treated seed through threshing machines or drills previously infested by diseased grains, nor to put cleaned seed back into bags that previously contained them or other unclean seed. In some cases the conditions of temperature and moisture that favor the germination of the seed and those that favor the germination of the spores are different, and this fact points the way to a prophylactic measure, namely, planting the seed at a season when the soil temperature is not favorable for the germination of the fungous spores. Recent experiments by Reed and Faris at the Brooklyn Botanic Garden have demonstrated that medium soil temperature, low soil moisture, and also a slightly acid soil were much more favorable for infection in the covered smuts of oats and barley, and loose and covered smuts of sorghum, than were higher moisture content and temperature and an alkaline soil. But these factors are interdependent, and "their interaction determines whether the infection will take place, and also the severity of the attack."[1]

Physiological Races.—One of the important recent developments of plant pathology is the discovery of the general occurrence among parasitic fungi of specialized races, that is, forms that appear essentially the same morphologically, but differ in the fact that they can grow on certain host plants but not on others—that is, they differ only physiologically. They are variously referred to as strains, forms, physiological races, physiological species, and otherwise.[2] A knowledge of this fact points the way to another method of disease control, namely, to plant in a given locality such variety or varieties of a given crop as are immune to the particular physiological race or races of pathogenes that are prevalent there. (See also p. 486.)

Resistant Varieties.—Just as certain persons appear to be resistant or even immune to certain human diseases, so certain varieties or even individual plants appear to be resistant to certain plant diseases, and *herein undoubtedly lies the best and the final*

[1] Reed, G. M. The smuts of cereals, etc. Brooklyn Bot. Gard. Record **13**: 103–124. July, 1924. Cf., also papers by Reed, and by Reed and Faris in Am. Jour. Bot. Vol. XI, Nos. 3, 7, 8, and 9. 1924.

[2] Our knowledge of physiological specialization has been summarized by Reed (Mem. Brooklyn Bot. Gard. **1**: 348–409, 1918). Cf. also, *Physiologic races of oat smuts*, by the same author in Am. Jour. Bot. **11**: 483–492. 1924.

solution of the problem of plant-disease control—namely, the planting of disease resistant varieties. Solution of the problem along this line also involves the breeding of varieties that are immune. A beginning has already been made in this work, but here lies open a vast and important field of research for the plant breeder and the plant pathologist. In the breeding of disease-resistant varieties it will be of the highest importance not to breed out, at the same time, other desirable qualities, such, for example, as high yield.

Plant Quarantines.—In order to prevent or reduce the spread of contagious plant diseases, the United States Government has established a strict quarantine on the importation from foreign countries of various species of trees, shrubs, vines, and herbaceous plants, known to be subject to certain plant diseases or insect pests, and therefore liable to introduce them into this country. Just as certain plants, not weedy in their native country, become troublesome weeds when introduced into a new country, so plant diseases and insect pests are often more virulent when introduced into a new country and become rapidly epidemic. The chestnut bark disease, and the White Pine blister-rust are recent cases in point. The Federal Horticultural Board now has inspectors at every port to inspect every importation of plants, and strict regulations are in force regarding what plants may be imported, and under what conditions.

In order to reduce the danger of infection from the blister-rust, and also from the pine-shoot moth (*Evetria buoliana*), the United States Department of Agriculture has issued quarantine regulations forbidding the importation of all five-leaved pines and all species and varieties of *Ribes*, except for experimental or scientific purposes by the Department of Agriculture. Since July 1, 1915, the importation of every species of the genus *Pinus* has been forbidden from all European countries and localities. In March, 1916, the Federal Horticultural Board requested all nurserymen in the eastern United States not to ship white pine, gooseberry, or currant stock into the Rocky Mountain and Western white pine forest areas. Later, by Federal and State quarantine regulations, the interstate shipment of pines, currants, and gooseberries was legally restricted, with a view to prohibiting the importation of any stock from infested areas into areas not infested.

Some, if not all, of our worst plant diseases have been imported. Rice smut traveled from Japan to South Carolina in 1898, the chrysanthemum rust from Japan through England (1895) to America (1896), and the potato blight from Chili to Colorado and across North America to Europe (1845). The downy mildew of the grape is an example of a disease probably originating in North America, where it has been known from the earliest times, travelling thence to France (1873), and other parts of Europe, reaching as far as Greece by 1880, and to Brazil by 1890.

These brief references indicate the importance of maintaining a strict quarantine on plants at all our ports of entry.

HELPFUL BACTERIA

Bacteria and the Dairy.—Not all bacteria, by any means, are harmful to man. Many of the practices of the dairy, for example, are dependent upon the action of bacteria. This, in part, is thought to explain the peculiarly delicious flavor of June butter. The souring of milk is caused by the action of substances produced by the bacteria present in all unsterilized milk. In fact the familiar flavor of milk is due in large measure to the presence in it of certain bacteria and the substances they produce. When milk is obtained under strictly sanitary conditions ("certified" milk) it loses much, if not all, of its characteristic and familiar flavor. The ripening, flavoring, and other peculiarities of the various varieties of cheese are due in part to the fact that they ripen under the influence of different kinds of bacteria and molds. The "ripening" is caused, in part, by the action on the substance of the cheese of the enzymes peculiar to the various fungi and bacteria growing in it, and in part by the action of an enzyme (*galactase*) inherent in the milk from which the cheese is made.

Vinegar.—Cider vinegar is in every respect a plant product. It is formed from the juice of apples, and ripens or "ages" under the influence of bacteria. These bacteria produce an enzyme which causes "acetic acid fermentation." This is the acid to which vinegar owes its sourness. There is not room here to explain the process of vinegar making in detail. (*Cf.* p. 626.)

The Nitrogen Problem.—The rôle of fungi and bacteria in the nitrogen economy of plants has been discussed in Chapter XI on The Nitrogen Problem.

CHAPTER XXV

THE PROBLEM OF SEX IN PLANTS

Cell-division and Reproduction.—The essence of reproduction is the separation, from the body of the parent, of a cell or larger portion, which becomes the starting point of a new individual. In some of the lowest plants, such as certain species of bacteria, cell-division always results in reproduction; that is, the two halves of the divided, one-celled body always separate at the close of cell-division, thus giving rise to two new individuals. A little higher in the scale of life we find such plants as *Pleurococcus*, where cell-division *may* result at once in reproduction, but where there is also a marked tendency for the cells to adhere together at the close of division, thus forming a loosely organized, multicellular plant body (Fig. 327). A further advance is illustrated by *Spirogyra*, where the cells normally do not separate at the close of division, but remain together, end to end, producing a multi-cellular body in the form of a filament (Fig. 325). From this simple condition there are transitions to the flat thallus of the liverworts, the simple, leafy axis of the mosses, the leafless axis of the moss-sporophyte, and the leafy sporophyte of the ferns. Not that these forms are derived one from the other; but they illustrate various degrees of complexity from the simplest unicellular plant body to a complex, multicellular body. By a comparison of these forms, we see that while, in some of the lowest forms, cell-division always results in reproduction, in the higher forms it only paves the way to increasing the size of the given individual, that is, to growth. In other words, between cell-division and reproduction there is interposed the enlargement or growth of the multicellular parent.

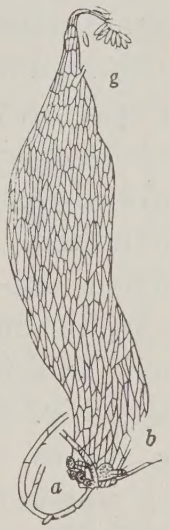


FIG. 386.—*Hymenophyllum* sp. Prothallus. *a*, antheridia; *b*, archegonia; *g*, gemmae. (After Winifred J. Robinson.) (Cf. Figs. 196 and 197.)

Vegetative Multiplication.—Attention has previously been called (Chapter XV) to the various methods by which the number of individual plants is increased by the separation of multicellular portions of the body of the parent. As in the case of the fern *Tectoria cicutaria* (p. 330), so in the fern *Woodwardia orientalis*, new plants arise from bulbils which form at numerous points on the upper surface of the leaves, always over a leaf-vein. The formation of gemmæ in Liverworts and Mosses is mentioned on page 305; they are also formed by the prothallus of some of the Filmy Ferns (*Hymenophyllaceae*), as shown in figure 386. In all these cases the number of individuals is vegetatively increased or multiplied, hence the term *vegetative multiplication.*

Reproduction by Spores.—In many plants, such, for example, as ferns, mosses, fungi, and others, the parent plant, while retaining its own vegetative organs intact, gives off individual cells (the spores), which become the starting points of new individuals. *The most distinctive thing about a spore is that it escapes, or becomes separated from the parent,* while all the other cells remain organically united.

When one-celled plants, like the bacteria or *Pleurococcus*, divide, the new daughter-cells correspond at the same time to spores and to entire plants. In other one-celled plants (*e.g.*, yeast, Fig. 92), the entire protoplast may become organized into spores, which escape from the cell-wall of the mother-cell. In a number of many-celled plants (*e.g.*, the alga, *Ulothrix*) practically every protoplast has the capacity of becoming organized into one or more spores which escape from the old cell-cavity (Fig. 387). The next higher step is the restriction of spore formation to certain cells in special organs (*sporangia*), while the other cells function only vegetatively.

Through all the variations of reproduction by spores there is, as a rule, only the separation of protoplasts from the parent body, never a cell-fusion. In all such cases nothing is introduced into the reproductive cell that was not in the parent; all of its potentialities are inherited from one parent and, with rare exceptions, the organism into which this cell may develop will closely resemble the organism from which it came.[1] (See also pages 305–307.)

[1] There are two possible exceptions which occur in comparatively rare cases. 1. In the formation of the reproductive cell by cell-division some-

Cell-fusions.—Some plants such as *Ulothrix* (Fig. 387), have been found to produce two sizes of spores, and two of the smaller spores must always unite before they can develop into full-sized,

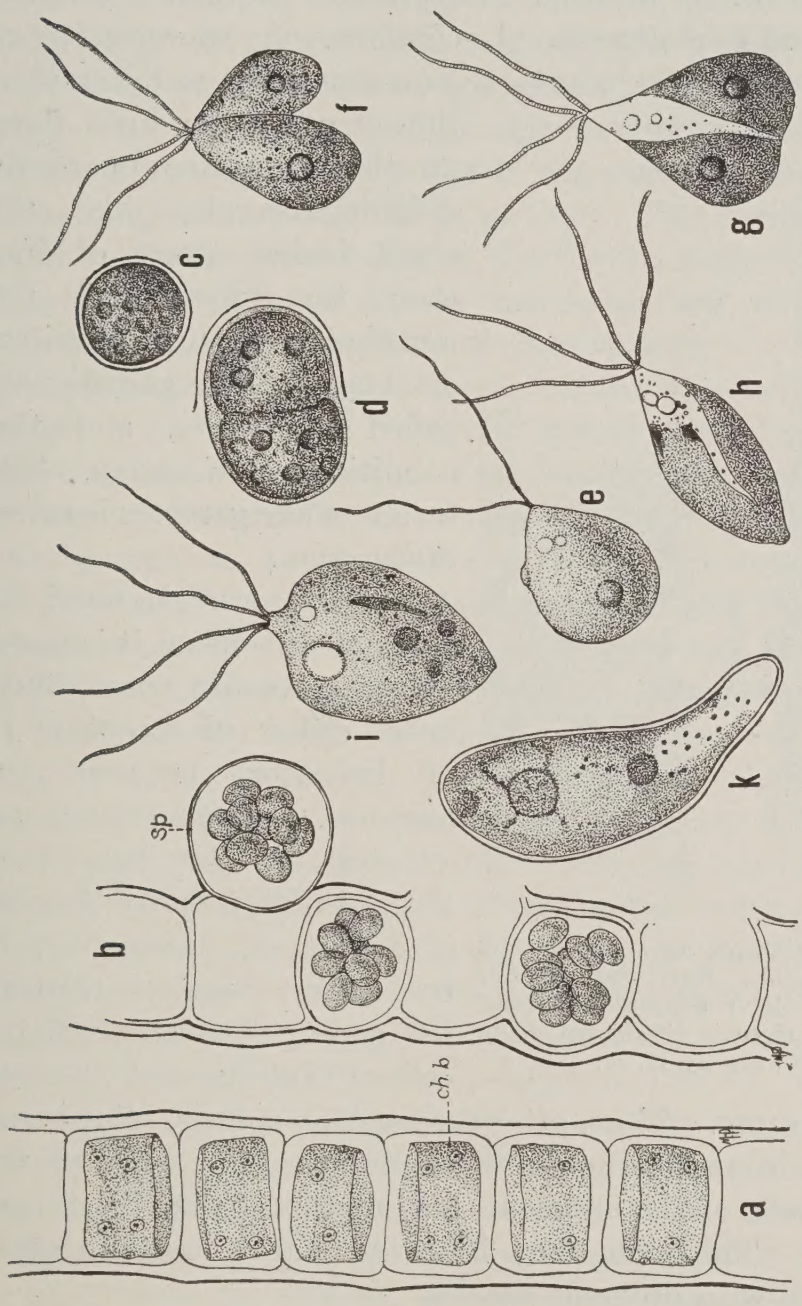


FIG. 387.—*Ulothrix zonata*; *a*, portion of the filamentous plant-body, showing the chlorophyll band (*ch.b*) in each cell; *b*, the various cells functioning as sporangia; from the upper cell the mass of small zoöspores, or gametes, (*sp*) are escaping; *c*, zygote; when the zygote germinates it produces several zoöspores, each of which develops into a new plant; *d*, beginning of germination of zygote; *e*, isogamous gamete; *f–h*, stages in the conjugation if isogamous gametes; *i*, large zoöspore; *k*, large zoospore germinating. (*c–k*, after Oltmanns.)

thing may be lost, which will result in a corresponding loss of characters in the adult organism. For example, color factors may be lost. 2. Some change may take place resulting in the expression of one or more new characters. This has been observed, for example, in bacteria, yeasts, and molds.

mature individuals.[1] Here a new feature of profound importance is introduced into the life history of the organism—a process by which potentialities or inheritances from two individuals are united in one. As noted in Chapter 18, reproductive cells that fuse with others in order to reproduce are called *gametes.*

Maleness and Femaleness. 1. *Ulothrix.*—As we ascend from simpler to more complex plants we find a progressive differentiation of gametes. First there are those that are apparently indistinguishable, like the small fusing spores of *Ulothrix;* the difference is not morphological but physiological only. Like gametes are called *isogametes,* and this condition is *isogamy.* The fusion of like gametes is called *conjugation.*

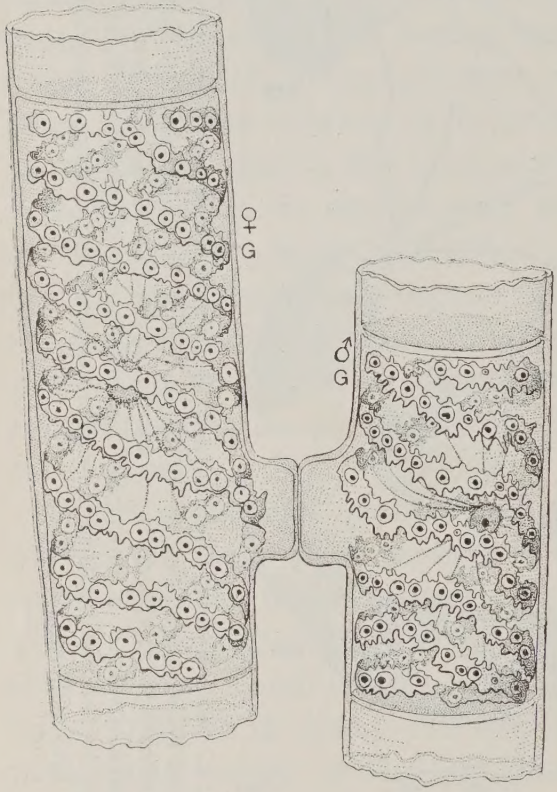


FIG. 388.—*Spirogyra sp.,* illustrating sexual differentiation. Receiving (female) gamete at the left; supplying (male) gamete at the right. (Redrawn from camera lucida drawing by H. H. York.)

2. *Spirogyra.*—In nearly all cases of cell-fusion it is possible to recognize some difference, either of structure or of behavior, between the gametes. In *Spirogyra,* for example, it has long been noticed that, if one of the cells of a filament passes over to the other filament through the conjugation-tube, *all* the cells of that filament will ordinarily do the same. Thus, after conjugation is over, *all* the conjugating cells in one filament will be found empty, while all the conjugating cells of the adjacent, conjugating filament will contain zygotes. This behavior, however, varies under certain conditions and with different species.

Studies by York have revealed the fact that the supplying gamete of *Spirogyra* always possesses less starch and a less num-

[1] In certain cases (*e.g., Ulothrix*) the microspores may develop small imperfect individuals without fusion.

ber of starch-formers (*pyrenoids*) than does the receiving gamete (Fig. 388). It has also been noted that the supplying filaments (male?) are less vigorous, vegetatively, than the receiving filaments (female?).

3. *Vaucheria.*—In the alga *Vaucheria*, as noted in Chapter XXI (Fig. 323), two kinds of gametes are easily recognizable; very small rapidly swimming ones, and relatively large immotile ones. Here the large one (the egg) remains in the oögonium, and fusion is accomplished by one of the smaller gametes or sperms swimming to and into the large one. The condition of having unlike gametes, *heterogamy*, is the rule in some of the algae and molds, in liverworts, mosses and ferns, and in all the higher plants, both gymnosperms and angiosperms.

4. *Sexuality in Molds.*—Sexual differentiation in the molds, which is physiological only, and not manifest by any apparent physiological differentiation, has been noted on page 470.

Sexual Differentiation of Spores. 1. *Physiological.*—When the spores of a plant are all alike, morphologically and physiologically they are called *isospores*, and this condition or phenomenon is called *isospory* or *homospory*. Yeast, bacteria, and certain algae, fungi, and ferns are *homosporous*.

The first step toward a differentiation of spores appears to be physiological. That is, certain plants produce spores that appear alike in size and structure, but behave differently, some developing into male gametophytes and some into female. This is the case in some of the mosses, and in the liverworts and horsetails. In the heterothallic molds a still simpler condition exists, for the mature plants that develop from the spores are indistinguishable in appearance and structure, but function in conjunction as plus and minus strains (p. 470).

Studies carried on by Buller and under his direction[1] have demonstrated physiological differences in the sexual value of the spores of Hymenomycetes. A method has been devised for removing the four spores from a living basidium (Fig. 359) and sowing them separately. By the use of this method it has been shown that in one of the Ink-cap fungi (*Coprinus lagopus*) one

[1] Buller, A. H. Reginald. Experiments on sex in mushrooms and toadstools. Nature **114**: 826. Dec. 6, 1924.

pair of the four spores on some of the basidia have one sex value, while the other pair are, physiologically, of the other and opposite sex. On other basidia the four spores were found to have four different kinds of sexual reaction, each spore differing from the others. In another species of *Coprinus* all the basidia have been found to be exactly alike, bearing only two kinds of spores, two of one sex and two of the other.

2. *Structural.*—When we come to the Little Club Mosses (species of *Selaginella*) we are introduced to a new phenomenon. The sporophytes, as we have seen in Chapter XIX, bear two kinds of spore-cases—one bearing relatively large spores (*megaspores*), the other bearing relatively small spores (*microspores*). This condition is called *heterospory.* The microspores give rise to male gametophytes; the megaspores to female gametophytes.

Differentiation of Sex Organs.—In many lower plants there is no recognizable structural difference between the organs that produce the heterogametes, but a step in advance in this direction is found in such a plant as *Vaucheria* (Fig. 323), where the antheridia are structurally very unlike the oögonia. This differentiation is carried a step further with the appearance of the multicellular archegonium in liverworts and mosses.

Structural Differentiation of the Sexes. 1. *Partial.*—In some species (though not in all) of the fresh-water alga, *Oedogonium,* the spores are unlike. Large zoöspores produce normal-sized plants that bear eggs and smaller *androspores.* The androspores, intermediate in size between sperms and zoöspores, produce smaller, *male individuals* only, of simple structure, which fasten themselves to the egg-bearing plants, and give rise to sperms, which fertilize the egg.[1]

2. *Complete.*—In the liverworts and mosses commonly, and in the higher plants always, the gametophytes are clearly differentiated into male and female, with unlike vegetative characters which clearly distinguish them. These unlike structural features are called the *secondary sexual characters.* In these groups the sporophytes are not differentiated in structure, but the spores they produce, though structurally alike, are

[1] It has been suggested that these androspores might be regarded as sperms developing without fertilization, *i.e.*, by *parthenogenesis.*

physiologically unlike, some producing male gametophytes, others female.

The most complete expression of maleness and femaleness is found in certain seed-bearing plants, where the sporophytes are differentiated into *microsporophytes* (staminate plants), bearing only microspores (young pollen-grains) which produce male gametophytes (mature pollen-grains), and *megasporophytes* (pistillate plants), bearing chiefly megaspores which produce female gametophytes (the endosperm of Gymnosperms, and the embryo-sacs of Angiosperms). Usually the two kinds of sporophytes are essentially alike, except for the sporophyll-bearing branches (the flowers), but the male and female gametophytes are as unlike as could well be imagined. Illustrations of this condition are the Gymnosperms (zamia, cycads, ginkgo), and the Angiosperms (willow, poplar, hop, etc.).

Chemical Differences of Sex.—It is only reasonable to infer that structural differences in individuals of unlike sex must be an expression of chemical differences in their protoplasm. It has, in fact, been determined that the sexually distinct plus (+) and minus (−) strains of certain molds (*Mucor* and *Phycomyces*) differ in their power of reducing and assimilating cane sugar and other sugars, thus indicating a difference in the amount or kind of enzyme present. In 1905 Gosio found that living cells can absorb and reduce the salts of tellurium and selenium (*e.g.*, Na_2TeO_3, K_2TeO_3; Na_2SeO_3, and K_2SeO_3). This is known as the "vital reaction" of Gosio. As previously noted, experiments of Satina and Blakeslee[1] give evidence that, on the average, the (+) sex of Mucors has a greater power to reduce the salts of these elements than has the (−) sex. This entire subject needs further experimental study.

Determination of Sex. 1. *Effect of Nutrition.*—Nobody knows the real cause of sex—of maleness and femaleness. We may arrange plants (and animals) in a series so as to show the gradual transition from the simple nonsexual condition to complete differentiation of males and females, but in doing this we should clearly recognize the fact that we have really explained nothing. We have only described events and structures in the order in

[1] See footnote on page 471.

which it seems probable that they have occurred, in the gradual development of the earth's vegetation.

But while we have never yet been able to determine in advance the sex of a plant or animal, we have been able to determine which sex shall gain expression. For example, we have seen above that male plants are frequently less vigorous and more poorly nourished than female plants. We would, therefore, expect that poor nutrition would cause a suppression of femaleness, and this is precisely what has been found in certain experi-

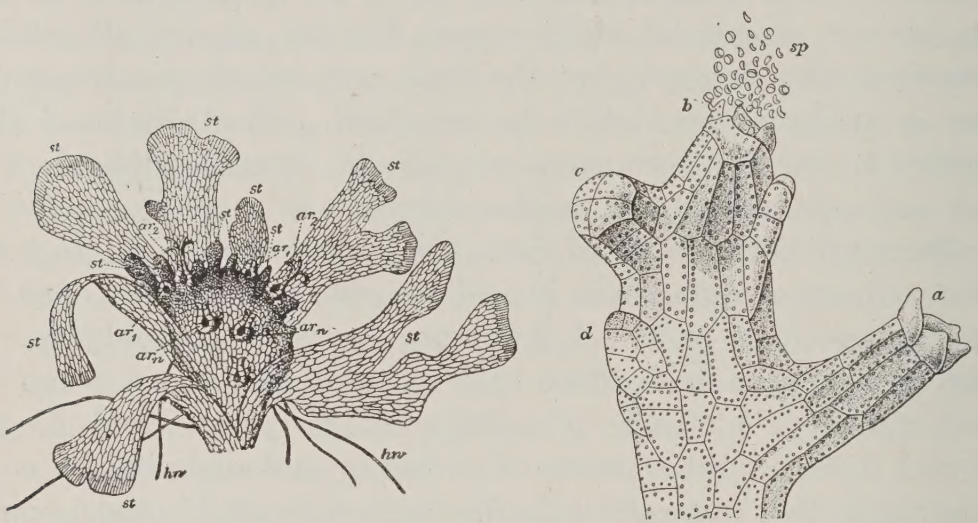


FIG. 389.—At left, female prothallus of *Equisetum arvense* L. ar_1, young archegonium; ar_2, archegonium before fertilization; *st*, sterile lobe of prothallus; *hw*, rhizoids. Several lobes were removed in order to show the cushion and the archegonia. Enlarged about 20 times. (After Sadebeck.)

At right, *Equisetum palustre*. Portion of a male prothallus, bearing antheridia; *a*, *b*, *c*, three antheridia in successive stages of development; *a*, empty; *sp*, escaping sperms and sperm-mother-cells; *c*, antheridium not yet opened; *d*, initia stage in the development of an antheridium. × about 70. (After Sadebeck.) Note the difference in enlargement; the female prothallus is, in reality, much larger than the male.

ments that have been made. When the prothallia of certain ferns that normally bear both antheridia and archegonia are grown under conditions that result in their being poorly nourished, the antheridia develop, but not always the archegonia. In such cases we know that we have not changed the sexual nature of the prothallus, but have only modified its expression.[1] This is

[1] In exceptional cases, perfect flowers may appear on staminate or pistillate plants, as in papaw (*Carica Papaya*), willow, and many others, suggesting that dioecious plants may, in reality, be of double sex-value, but that only

further illustrated in the gametophytes of the Horsetails (*Equisetum*) which are usually differentiated into larger ones (female) and smaller ones (male) (Fig. 389); but under certain conditions (apparently involving differences of nutrition), the female gametophytes may bear antheridia, and the male gametophytes archegonia.

2. *Effect of Constitution of Germ-cells.*—If sex is not determined by external conditions—by environment—then its explanation must lie in the internal constitution of the germ-cells—in their chemical, physical, and morphological differences. Remarkably

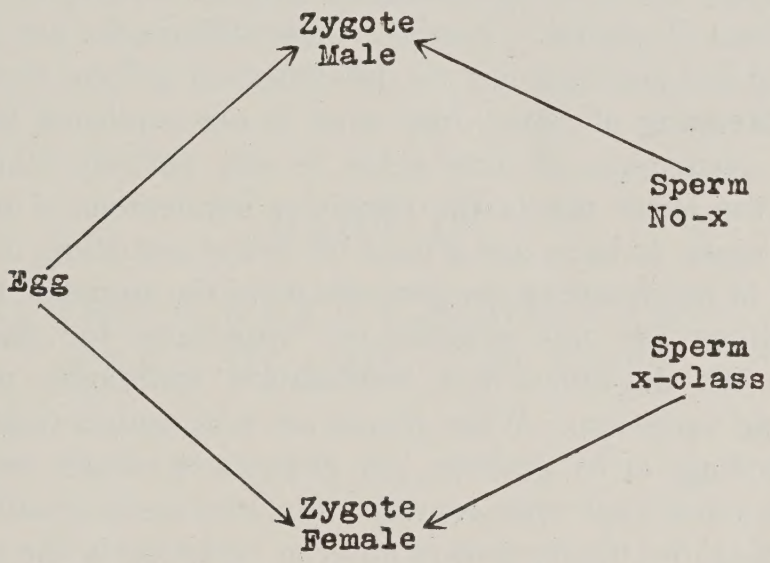


FIG. 390.—Diagram to illustrate determination of sex by the X-chromosome.

careful and accurate observation has, in fact, revealed a constant and fundamental morphological difference in the germ-cells of animals. It has been found, for example in some insects, that the nucleus of every egg possesses a certain clearly distinguished chromosome, called the X-chromosome, while in the sperms one-half possess it and one-half do not. This X-chromosome is always associated with femaleness. If an egg is fertilized by

---

one of the sexes comes normally to expression. By altering the nutrition, Schaffner (1922) was able to cause reversal from staminate to pistillate plants and *vice versa* in species of *Arisaema* (Jack-in-the-Pulpit and Green Dragon). Considerable evidence seems to indicate that "maleness" (staminateness) and "femaleness" (pistillateness) in flowering plants is a condition and not an inherited character.

a sperm possessing the X-chromosome a female zygote is determined, otherwise the zygote will be male, thus:

Egg X + sperm no-X = zygote X (male).
Egg X + sperm X = zygote XX (female).

This condition is illustrated diagrammatically in figure 390.

In sea-urchins, and some other animals, this condition may be reversed, the sperms being all alike and the eggs unlike. Careful investigations have, so far, failed to reveal the general occurrence of anything corresponding to the X-chromosome in plants, but undoubtedly there are fundamental differences between the eggs and sperms of plants. Possibly these differences are chemical only, and not accompanied by differences of cellular structure.

The Meaning of Sex.—Just what is accomplished for plants by the occurrence of two sexes is not entirely understood. Among the lower plants the primitive expressions of sex seem, in some cases, to have met a need for better nutrition, or to have resulted in rejuvenating the protoplasts of the gametes; but these explanations are not satisfactory, especially for the higher plants. We do know that fertilization commonly results in increasing variation. When plants are propagated vegetatively, as by cuttings or by grafting, the characters remain constant in the new plants,[1] but when reproduction is by seeds (resulting from fertilization) we nearly always observe variation in the offspring. This is, of course, an advantage, for it is only by variation that new characters may appear, and without the appearance of new characters there would be no opportunity for the improvement of plants—either by nature or by man.

The results of all studies and discussions of the question of sex lead us to recognize the fact that it is still largely an unsolved mystery. We must make further and more accurate observations, and be careful and logical in our reasoning, before we can hope to solve this difficult problem.

[1] Except in the special case of bud-sporting (p. 963 and Fig 674).

PART IV

THE GREAT GROUPS OF SEED-BEARING PLANTS

CHAPTER XXVI

PRINCIPLES OF CLASSIFICATION

Need of Classification.—The number of different kinds of plants is great—far beyond the imagination of one who has never studied or thought about the subject. But when we recall the tendency of plants to vary, and note that there are, almost certainly, no two individual plants exactly alike in the world—no two leaves exactly alike in form, dimension, and structure, no two organs of any kind exactly alike—and when we recall the fact that both aquatic and land plants have been reproducing and varying for untold thousands of years, in this and previous geological ages, then we begin to realize how extensive the diversity of types must be, and can appreciate the necessity of noting points of likeness and degrees of similarity, and of arranging individual plants in groups, based upon similarity in one or more characters. This arranging of plants into groups is called *Classification*, and the principles of classification constitute the science of *Taxonomy* from two Greek words,[1] meaning "arrangement" and "law." Since the classification of plants brings order out of apparent chaos, that phase of botanical science which deals with classification is also called *Systematic Botany*. Obviously, the different groups of plants must have names, and the principles governing the application and use of names constitute the laws of *Nomenclature*. The principles of classification are derived from a study of plants themselves, but the laws of nomenclature are (or should be) based upon convention, or agreement between those who make a professional study of classification.

Scientific Names.—Science is universal, and it is therefore highly important that a universal language should be used—at least in designating the different organs, individuals, and groups.

[1] Taxis (τάξις), *arrangement* + nomos (νόμος), *law*.

This is made all the more necessary by the fact that the terms used in daily conversation and non-scientific writing are seldom as accurately defined as the needs of scientific accuracy demand. To the layman, or the non-scientific writer, for example, practically all underground parts are "roots," no distinction being made between true roots and rhizomes, which are underground stems. The layman speaks of "Dog's-tooth-violet," which is not a violet at all, and not even related to the violet; the name would not be understood in another country, whereas *Erythronium*, the Latin name for the plant, is understood the world over, wherever plants are scientifically studied. Again, a common name may designate one kind of plant or animal in one country, and another plant or animal in another country, or in another part of the same country. Thus, the word "robin" designates quite different kinds of birds in England and America; "daisy" means a certain kind of plant in Europe, but a quite different kind of plant in the United States. In England Sycamore means an *Acer* (called maple in America); in America Sycamore means *Platanus;* the sycamore of the Bible is a species of *Ficus* (one of the figs.).

"Bittersweet" may mean either *Celastrus scandens* (Celastraceae) or *Solanum Dulcamara*, of the Solanaceae. To people living near the seashore "eel grass" means a marine plant (*Zostera marina*) belonging to the Potamogetonaceae, but inland, generally, "eel grass" designates the fresh water form, *Vallisneria spiralis*, of the Hydrocharitaceae. In some cases, a Latin generic name is used as the common name for a quite different and unrelated species. Thus, the Indian cress (*Tropaeolum*, of the Tropaeolaceae) is commonly known to gardeners by the name "Nasturtium," which is the scientific name of the genus of the cresses in the Cruciferae. In a quite similar manner the generic name of the lilac (*Syringa*, of the Olive family) is used as the "common" name for *Philadelphus*, a shrub of the Saxifrage family. "Blazing star" is used to designate the spring-flowering *Chamaelirium luteum* (Liliaceae) and also the fall-flowering *Liatris squarrosa*, of the Compositae. Examples might be multiplied, showing how indefinite and even misleading the "common" names of plants may be, and therefore the need of so-called "scientific" terms—that is, terms accurately defined, belonging to an international language, having the same form and meaning

in all places—even in countries that have different languages, and used uniformly wherever science is studied.

Systematic Groups. *a. Species.*—We have just noted that no two individual plants resemble each other exactly; if they did we could not tell one plant from another. But, disregarding these differences (the differences that enable us to distinguish individuals), and disregarding certain exceptional variations to be noted in Chapter XL, the offspring of a given plant resemble the parent or parents so closely *in certain essential characters* that we recognize them more or less readily as being the same *kind* of plant. Thus, for example, all roses are near enough alike so that we may readily say of a plant—"this is a rose;" all moss-roses are near enough alike so that when we see a specimen we are able to say at once, "This is a moss-rose." Plants which are essentially alike in the majority of their fundamental structural characters, and which, in reproduction through a series of generations, produce offspring having the same fundamental characters as themselves, belong to the group designated as a *species.* This fact was succinctly stated by the noted French botanist Jussieu,[1] who defined species as, "*the perennial succession of similar individuals perpetuated by generation.*

Objectively, then, a species is a *group* of individuals, continuing through time as well as occupying space; subjectively, however, a species is a *mental concept* formed by observing and comparing large numbers of individuals. By comparison we note what characters are significant and common to all the individuals, and combine these characters into our concept of the species, disregarding for the time being the non-significant, accidental characters. Thus, red clover is red clover, though in a meadow (Latin, *pratensis*) some of the clover plants may have lighter or darker red flowers than others, may be larger or smaller than others, may blossom and seed earlier or later than others, or

[1] Antoine Laurent de Jussieu (1748–1836). First director of the *Jardin des Plantes*, Paris (1793). In his *Genera plantarum* (1789) he adopted three main groups of plants—Acotyledones, Monocotyledones, Dicotyledones—and under these groups, *for the first time, he described plant families* (long called orders), one hundred in number; under the families he described the genera. Linnaeus declared himself unequal to that task. Jussieu was called, by his contemporary, Richard, "the first botanist in Europe."

may have more or fewer leaves than others; size, precise shade of color, date of flowering, and number of vegetative parts are not essential to the concept, "red clover." From similar considerations it is more strictly accurate to say of any individual specimen, "This *represents Trifolium pratense* (red clover), than to say, "This *is Trifolium pratense.*"

b. Genus.—But there are other kinds of clover besides red clover. We easily recognize the fact that they are clover because of certain characters they do possess, while with equal ease we see that they are *not red* clover, because of characters they do not possess. They belong to a *different species* of clover, but nevertheless they are clovers. Thus we rise to a group of a higher order—the *genus* or kind (as distinguished from particular or "specific" kind). Objectively, then, a genus is a group of species, subjectively it is a clearly defined concept, embodying the essential characteristics common to all the related species. The *generic name* for clover is *Trifolium*, referring to the fact that all true clovers, as a rule, have compound leaves of *three leaflets.*

Every species of plant or animal has two names—its generic name, and its specific name. Thus, in *Trifolium* (clover), we have:

Trifolium pratense, Red clover
Trifolium repens, White clover
Trifolium hybridum, Alsike or Alsatian clover, etc.

In this connection we see another striking illustration of the inadequacy of "common" names for scientific purposes, for the so-called sweet "clovers" are not clovers at all, but melilots; *i.e.*, they do not belong to the genus *Trifolium*, but to the genus *Melilotus.* "White sweet-clover" is *Melilotus alba*, and "Yellow sweet-clover" is *Melilotus officinalis*, "officinalis" meaning the one which is used as a *drug* (dried plant) in medicine.

c. Groups of a Higher Order.—Just as different species are grouped in genera, so genera are grouped in *families*, families in *orders*, orders in *classes*, classes in sub-divisions, and the latter in *divisions* of the plant *kingdom*, thus:

Kingdom—*Plantae* (plants)
Division—*Spermatophyta* (plants that bear seeds)
Sub-Division—*Angiospermae* (seeds enclosed)
Class—*Dicotyledones* (seeds with two cotyledons)
Sub-Class—*Polypetalae* (petals distinct to base)
Order—*Rosales* (Carpels distinct, *i.e.*, ovary simple)
Family—*Leguminosae* (fruit a legume)
Tribe—*Trifolieae* (leaves trifoliolate, denticulate)
Genus—*Trifolium* (flowers in heads or umbels)
Species—*T. pratense* (flowers red, etc.)
Variety—*T. pratense perenne* (perennial clover)

As a rule the names of orders end in *-ales*, and the names of familes in *-aceae*, though there are exceptions to the latter, as in Leguminosae, Gramineae.

Natural versus Artificial Classification.—There are two bases for the classification of plants and animals. Recognizing that all plants are derived by descent (with modification) from pre-existing plants, a "natural" classification aims to arrange the various groups in such a way as to show their relationship to each other. On this basis all the characters are considered, and the different groups (species, genera, orders, etc.) come next to those which they resemble in all apparently *essential* characters.

An artificial classification would disregard the fundamental fact of descent with modification, and would arrange living things in groups on the basis of some one character, arbitrarily chosen, and which might or might not be significant, as if a collector of postage stamps should arrange his stamps on the basis of color rather than by countries. Thus, an early system of classification arranged plants into herbs and trees (on the basis of having or not having perennial stems). Linnaeus, the great classifier, based his classification of plants on the number of stamens. On that basis plants wholly unrelated by nature would fall into the same group.

Historical.—Theophrastus (370–285 B.C.) has been called the "first of real botanists in point of time." He was a pupil of Aristotle and was in charge of the so-called "botanic" garden,

near Athens. In his *History of Plants* he described about 500 species, mainly of cultivated plants, and classified them into trees, shrubs, undershrubs, and herbs.

From the time of Theophrastus little progress was made in plant classification until the Sixteenth Century, when Leonhard Fuchs (1501–1566), in his *Stirpium Historia*, arranged his plants alphabetically by their Greek names. Hieronymus Bock, also

FIG. 391.—Linnaeus, the great classifier (1707–1778). He is wearing a sprig of the twin-flower (*Linnaea borealis*), one of his favorite flowers, and named after him by his friend, Gronovius. He is regarded as the father of modern systematic botany.

known as Tragus[1] (1498–1554), criticized the alphabetical arrangement of Fuchs, contending that "such forms as nature seems to have linked together by similarity of form," should be grouped together. He classified in three groups, herbs, shrubs, and trees.

Gaspard Bauhin (1560–1624), in his *Pinax Theatri Botanici* (1623), named genera without describing them, and gave very brief descriptions of species. He kept seaweeds, trees, shrubs,

[1] Bock (German) and Tragus (Latin) both mean "goat."

grasses, and "lilies" in separate groups, but gave no name to groups higher than genera.

John Ray (1627–1705) one of the most famous of English botanists and forerunner of Linnaeus, retained "woody" plants and herbs as his main divisions, He was the first to make the number of cotyledons a basis of classification, and sub-divided "flowering herbs" (but herbs only) into monocotyledons and dicotyledons.

Tournefort and Linnaeus did not adopt the improvements introduced by Ray. Tournefort (1656–1708), professor of botany at the Jardin du Roi during the reign of Louis XIV, in his *Institutiones Rei Herbariae* (1703), first described genera. His major groups of plants were each subdivided into *Petalodes* (those having petals) and *Apetali* (those without petals).

Linnaeus systematically described species, and was the first to adopt a uniform binomial nomenclature.[1] His "Sexual System" of arrangement was based on the number of stamens and pistils, and his great work *Species Plantarum* (1753) is taken as the starting point of modern botanical nomenclature.

To follow the history of classification from Linnaeus to the present day would lead us too far into details for the purpose of this book.

Linnaeus recognized the desirability of a *natural classification*, but acknowledged his inability to make a natural arrangement of genera. This was first accomplished, with any degree of success, by Antoine Laurent de Jussieu, in 1789.

Our knowledge of plants is not sufficient to enable us to make a perfect natural classification; all that we can do is to approximate this as nearly as possible, and to continue our endeavors to perfect the natural system by continued investigations of plant structure and affinities.

In the following chapters some of the principal agricultural plants are chosen to illustrate the various plant families as at present recognized by botanists.

[1] Binominals were in use long before Linnaeus, but they were not employed in a uniform, consistent manner. Linnaeus employed binominals as the standard method of designating species, and their general use dates from the publication of his *Species Plantarum* (1753). Later it became customary to add the name of the author to the Latin name or combination. (*Cf.* foot-note, p. 727.)

CHAPTER XXVII

EVOLUTION AND CLASSIFICATION[1]

In the preceding chapter we have noted that a natural classification of plants aims to arrange the various groups in such a way as to show their genetic relationship to each other. To do this it is necessary, not only to study plant structure, but to have some conception of the probable order in which the various groups of plants have appeared during the evolution of the plant kingdom—to know which are the earlier and more primitive, and which the later and more highly developed. In other words a knowledge of the *course* of plant evolution is essential to a proper classification. If we had specimens of all the different kinds or groups of plants that have appeared from the beginning, the task of a natural classification would be greatly simplified. The available evidence, however, is incomplete and fragmentary, and so we can only approximate the truth.

Sources of Evidence.—Evidence as to the probable course of plant evolution and therefore the probable relationship of the great groups of plants may be derived, in part, from the following sources:

1. Comparative anatomy of living forms.
2. Structure of fossil forms in comparison with each other and with living forms.
3. Geological succession of fossil forms.
4. Comparative life histories of living forms.
5. Geographical distribution of both fossil and living forms.

Without attempting anything like a thorough analysis of the evidence now in hand from these various sources, and confining our discussion to the seed-bearing plants, it may be stated that the trend of evolution in these plants has been substantially as follows:[2]

[1] Dr. Alfred Gundersen, Curator in the Brooklyn Botanic Garden, is joint author of this chapter.

[2] The subject of the evolution of plants is treated more extensively in the author's earlier book, *Heredity and evolution in plants.* Philadelphia. P. Blakiston's Son & Co. 1920.

The Stem.—An examination of fossil plants reveals the fact that nearly all seed-bearing plants of earlier geological periods had woody instead of herbaceous stems. Of course woody stems would be more readily preserved as fossils, but still fossil remains of herbaceous flowering plants exist. They are wholly unknown in the Primary or Paleozoic rocks, the upper strata of which include the Carboniferous and Permian formations, and they have not yet been, for a certainty, found in the Cretaceous Period, which includes the later rocks of the Secondary or Mesozoic Era. So far as definitely known, they first appear in the Tertiary periods of the Cenozoic Era, that is, the periods that preceded the Ice Age. In the Tertiary of Switzerland about 24% of the Angiosperm fossils are herbaceous. The evidence from fossil plants is not conclusive, but it favors the theory that woody plants are more primitive than herbaceous.

Studies in comparative anatomy indicate that the continuous layer of wood, which is characteristic of modern trees and shrubs, is a more primitive character than the separate vascular bundles which characterize herbaceous stems. In other words, the more woody the stem the more primitive the species. Again, groups of plants that must be considered the more primitive on the basis of other evidence are found also to be composed largely of woody rather than herbaceous species.

Studies of the comparative histology of the stem lead to the conclusion that scalariform-pitted vessels are more primitive than porous vessels. Exclusively scalariform vessels occur in comparatively few families—notably the magnolia, witchhazel, saxifrage, dogwood, honeysuckle, holly, heath, and tea families—all, on the basis of other evidence, considered as primitive. Moreover, the scalariform pits characterize most of the earliest fossil angiosperms, and must be considered as the primitive type.

In short, the evidence seems to justify the conclusion that herbaceous and woody plants which have porous pitted vessels have been derived by descent (with modification) from woody ancestors having scalariform vessels. The prevailing types today are *woody* plants with porous vessels. Thus the Gymnosperms, the lowest seed-bearing plants, fossils of which far antedate the flowering plants, have no herbaceous forms. In the sympetalae, the highest of the seed-bearing plants, the propor-

tion of herbaceous species is very much greater than in the more primitive group, the Polypetalae. In groups comprising both woody and herbaceous forms, such as the Pea Family, the herbaceous forms have the most advanced floral structures. Moreover, the time of one generation (from seed to seed) is much longer with trees and shrubs than with herbaceous Angiosperms so that, in a given long period we might expect a more rapid evolution, and therefore a larger number of genera, among herbaceous forms. But more than half the families of Dicotyledons contain no herbs, and there are only slightly more than half as many genera of herbaceous dicotyledons as of woody plants (about 2600 genera of herbaceous dicotyledons as against about 4000 genera of woody plants). These facts suggest that the herbaceous forms are a later development than the woody. Herbaceous angiosperms, however, are not a single group; they must have arisen from various woody ancestors.

Leaf.—Just one genus of gymnosperms, *Gnetum*, possesses the typical simple leaf of the dicotyledons. Divided and compound leaves must be considered as derived forms. Embryonic leaves (cotyledons), which always manifest primitive characters, are entire, even in plants that have compound foliage leaves.

Flowers.—Single flowers, as in buttercups, and loose inflorescences, as in mustard, are considered primitive; dense inflorescences, especially umbels (Queen Anne's lace), and heads (daisy, sunflower) are considered advanced forms.

A great majority of the angiosperms have the floral parts arranged in whorls. In several of the families of the magnolia group (although in the genus *Magnolia* the floral envelopes are cyclic), in the cacti, and in a few other families the parts are more or less spirally arranged, doubtless the more primitive form (Fig. 410).

Following the appearance of the whorled arrangement of flower parts, there begins to appear more or less *cohesion* of the parts and also *adhesion* of the adjacent whorls.

Perianth.—A distinct calyx and corolla is usual among flowering plants. The absence, as in magnolia and lily, of a marked distinction, must be considered more primitive.

So-called united petals have not really united. What happens is that there is a "zonal" development from the receptacle or base of the flower, resulting in a continuous, more or less tubular

corolla or calyx, as in the morning-glory or bellflower. The first parts of the sympetalous corolla to appear, however, are the separate tips. In other words, the sympetalous flower, in the course of its formation, begins as polypetalous, apparently a recapitulation of the evolutionary history. In dandelion and other composites the five petals are represented by the five teeth at the edge of the strap-shaped corolla.

United sepals occur much oftener than united petals. In fact separate sepals are the exception. They are found generally in three orders: *Ranales* (buttercup), *Parietales* (rockrose, violet), and *Papaverales* (poppy).

The early flowers were doubtless regular, that is, having all the parts in a whorl similar, while irregular or *zygomorphic* forms, such as foxglove, are an adaptation to insect visitors, facilitating cross-pollination: these must be derived forms.

The color and fragrance of flowers are also considered as adaptations to insect visitors. The green and yellow colors apparently preceded the red, purple, and blue.

Stamens.—In the *Polypetalae* there are generally two whorls of stamens, though the Umbellales (dogwood) have only one. The *Sympetalae* have only one whorl, except the Ericales (heaths) and Ebenales (persimmons). In the *Primulales* (primroses) there is often only one whorl evident, but then the stamens are situated opposite the lobes of the corolla, and traces of an alternate whorl can often be found.

In the *Polypetalae* and in the *Ericales* the stamens usually arise from the receptacle. In the *Sympetalae* the stamens usually are epipetalous, that is, growing out from the corolla tube, obviously the derived form.

The stamens are also sometimes united; either the filaments form a tube, as in the Mallow Family, or the anthers unite, as in the Lobelia and Composite Families. It is of interest that united stamens occur also in the strange gymnosperm, *Welwitschia*, a native of South Africa. In the orchids the stamens and pistil grow together on a common structure, a specialized arrangement.

Carpels.—In the Gymnosperms the carpels (seed-bearing scales) are separate. Separate carpels, in the Angiosperms, occur chiefly in the magnolia group and in the Rose Family, an important evi-

dence that these families are primitive. Sometimes the bases of the carpels cohere slightly, as in geranium, with the styles separate; more often the styles and stigmas are also united, as in primrose. The compound pistil is obviously the more advanced form.

Numerous ovules to a flower are more common in the lower families. Fewer cells per ovary and fewer ovules per cell appear in higher groups. A single ovule to a flower characterizes the most specialized groups, such as the composites. A reduction in the number of ovules in plants may be compared with the reduction of the number of eggs in animals. Among the fishes enormous numbers of eggs are laid, but only a few develop. Among the mammals, on the other hand, comparatively few young are born, but these are taken better care of. Among plants, as among animals, increasing care of the next generation appears to be an all-important principle. A single seed to a flower is also common among wind-pollinated plants.

The occurrence of birches and their relatives among the earliest Angiosperm fossils, the structure of their wood (in many ways suggesting the *Gnetales*), their wind pollination, and their cone-like inflorescence, assign to them a place among the primitive Angiosperms, but other evidence has led to an opposite conclusion. The whole question needs further investigation.

The mode of attachment of the ovules is called *placentation*, the region of attachment of the ovule being called a *placenta*. The ovules are usually borne on the margin of the carpellary leaves. With the carpels closed to form a compound pistil, the ordinary *axile* placentation results. *Parietal* placentation, as in rockrose, violet, and poppy, and *central* placentation as in pink and primrose, are probably derived forms.

Where the three outer whorls of the floral envelope develop more or less together, an *inferior* ovary results. This advanced form characterizes the great orders, *Umbellales* (dogwood), *Myrtales* (myrtle), *Rubiales* (honeysuckle), and *Campanulales* (bellflower and composites), and a few other groups.

Considering the flowering plants as a whole, two great tendencies appear to have been effective; a tendency to an increasing fusion of the parts, and a tendency to increasing adaptation to insect pollination.

Seed.—Evolution in angiosperms is believed to have proceeded from seeds with two seed-coats to those with only one. Most of the plants whose flowers have separate petals (*Polypetalae*), and also the Sympetalous orders of primroses and gourds, have two seed-coats. Most of the plants whose flowers have united petals (*Sympetalae*), and also the order of dogwood and carrot (*Umbellales*) have only one.

Evolution doubtless proceeded from seeds with endosperm (a store of food outside the embryo), as occurs in magnolia, pink, dogwood, and grasses, to seeds without endosperm, such as in the pea, gourd, sunflower, and others.

Embryos with two or more "seed-leaves" or cotyledons appear to be more primitive than those with one. The conifers have usually many cotyledons, the less primitive joint-firs (*Gnetales*) two. The great group of the Monocotyledons, with one cotyledon, represents almost certainly one or more branches from the early dicotyledonous plants.

A straight embryo, such as is found in most flowering plants, must be considered as simpler than a curved one, such as characterizes the pink, pigweed, four-o'clock, and other families.

Geographical Distribution.—A study of the geographical distribution of living Angiosperms shows that, for Dicotyledons, woody plants are the dominant type in the tropics, while herbaceous plants predominate in the temperate zones. Several families that include both woody and herbaceous forms and are represented in both tropical and temperate regions, have only herbaceous forms in the temperate zones. Such families are the Pigweed Family (*Amarantaceae*), Violet Family (*Violaceae*), Convolvulus Family (*Convolvulaceae*), Madder Family (*Rubiaceae*), the Composite Family (*Compositae*), and others. Now fossils of such tropical forms as Palms and Cycads are found in Cretaceous rocks outside of the tropics, even as far north as Greenland. This indicates that a tropical or sub-tropical climate then prevailed in these higher latitudes and that the (woody) vegetation of that time was adapted to a warm climate only. Herbs, on the other hand, are particularly adapted to endure the cold winters of the temperate zones, because of their short life cycle, often completed in one year or less. They may safely pass the winter in the form of seeds or, in the case of biennials

and perennials, by underground parts. These facts account, in part, for the prevalence of herbaceous types in temperate zones, and favor the inference that herbaceous dicotyledons are comparatively late forms which have descended from earlier and more primitive woody ancestors.[1]

It has been said that the "phylogenetic tree" of seed-bearing plants is like a living tree, in that the tips of the branches are herbaceous, while the lower parts are woody. The parts of the tree of evolution below the seed-bearing plants are again herbaceous, and the very lowest are water forms, the succession being somewhat as indicated below:

Herbaceous Angiosperms
↑
Woody Angiosperms
↑
Gymnosperms
↑
Ferns
↑
Liverworts
↑
Algae

The facts above noted are tersely expressed in the following tabular statement, in which the condition most common in existing plants is indicated by the words in capital letters.

TABLE XI.—COURSE OF EVOLUTION OF STRUCTURES IN SEED-BEARING PLANTS

STEM	CARPELS
WOODY to Herbaceous	Separate to UNITED
Vessels scalariform to POROUS	MANY CARPELS to few
PERIANTH	SUPERIOR OVARY to inferior
Spiral to CYCLIC	AXILE PLACENTATION to parietal or central
Separate Sepals to UNITED	
SEPARATE PETALS to United	
REGULAR to Irregular	SEED
STAMENS	MANY OVULES to few
Indefinite to DEFINITE	TWO SEED COATS to one
TWO WHORLS to one	ENDOSPERM to none
SEPARATE to united	Many Cotyledons to Two or one

[1] In the case of Monocotyledons the available evidence indicates that they were derived, at a comparatively late period in the evolution of the Plant Kingdom from Dicotyledonous ancestors.

CHAPTER XXVIII

THE FAMILIES OF FLOWERING PLANTS (ANGIOSPERMS): APETALOUS AND POLYPETALOUS DICOTYLEDONS

It is customary to divide the dicotyledonous flowering plants into three (more or less artificial) groups, as follows:

a. Apetalae.[1]—Petals wanting, except in the Portulacaceae (Purslane Family) and most of the Caryophyllaceae (Pink Family).

b. Polypetalae.[1]—Petals present (except that a few genera in several of the families have no petals).

c. Sympetalae.[1]—Petals partly or wholly united. In a few exceptional genera the petals are separate or wanting. This groups is also called, by some authors, *Gamopetalae.*

Apetalae

ORDER, Casuarinales

The order *Casuarinales* comprise only the Beefwood Family (*Casuarinaceae*), with one genus, *Casuarina*, found on the shores of the Indian ocean and throughout Australasia and Polynesia; also in Florida.

ORDER, Piperales

The *Piperales* are herbs or shrub-like plants, with flowers arranged on spikes (Fig. 392). Each flower is subtended by a bract. The order is represented in temperate regions only by the family *Saururaceae*, also with only one genus,—the Lizard's

[1] The Apetalae and Polypetalae are, by some writers, placed together in one group under the names *Choripetalae* (Greek, *chori* = apart + *petalon* = leaf or petal), or *Archichlamydeæ* (Greek, *archi*, first + *chlamys*, cloak, signifying the supposedly primitive type of floral envelope). The Sympetalae are, by some, called *Metachlamydeæ* (Greek, *meta*, after or later + *chlamys*, signifying a later or higher type of floral development).

tail (*Saururus*) (Fig. 393). It is interesting to note that, of the two known species of this genus, one occurs in eastern North America while the other is found only in eastern Asia. This is one of many striking cases of discontinuous geographical distribution, and illustrates a general fact of distribution first pointed out and explained by the great American botanist, Asa Gray,[1] namely, that the flora of eastern Asia is most closely

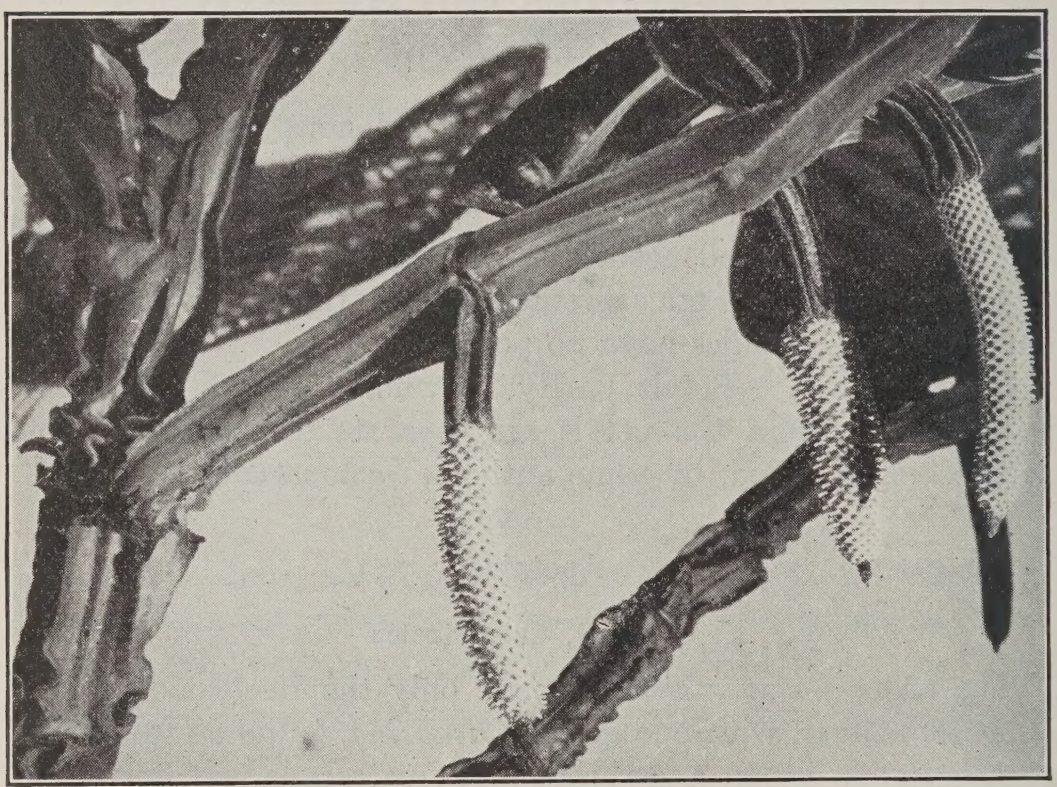


FIG. 392.—*Piper magnifica.* Portion of the shoot, one branch of which bears three spikes.

related, not to the flora of western North America (on the opposite side of the same ocean that washes the shore of Asia), but to the flora of eastern North America. The explanation of this fact, at first so puzzling to the student of geographical distribu-

[1] ASA GRAY. b. Nov. 18, 1810; d. January 30, 1888. Professor of botany and director of the Botanic Garden, Harvard University. He was the foremost American systematic botanist, and was an early defender of Darwin in America. With his teacher, John Torrey (1796–1873), he was among the first to abandon the Linnaean system of classification.

tion, is found in the events connected with the advance and retreat of the continental ice-sheet, during the glacial epoch.[1]

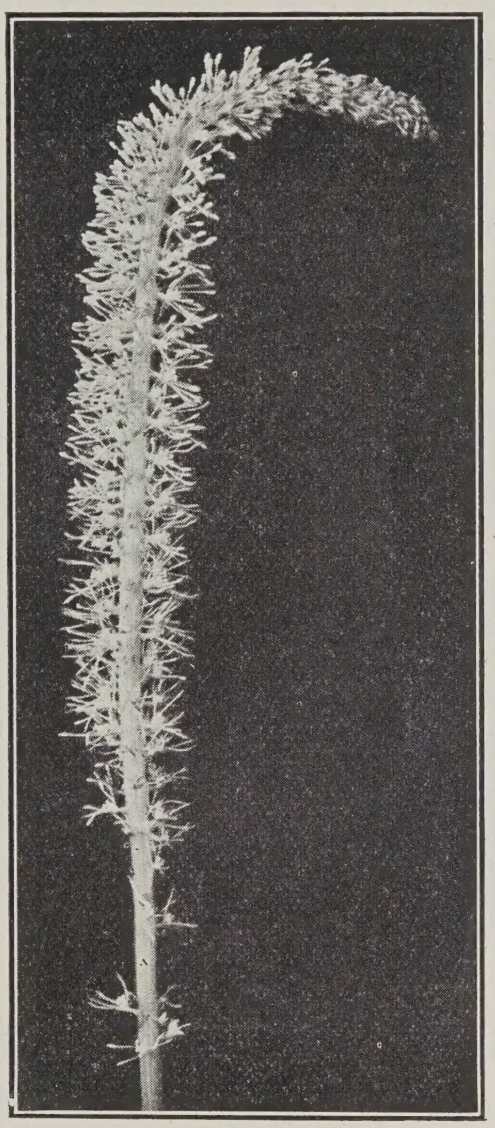


FIG. 393.—Lizard's-tail (*Saururus cernuus*). Inflorescence about natural size.

PEPPER FAMILY

The Pepper Family (*Piperaceae*) includes tropical and subtropical herbs, shrubs, and trees, many of which are aromatic

[1] For the details see, Gray, Asa. On the botany of Japan, and its relations to that of North America, etc. Botanical Memoirs, extracted from Vol. VI (New series) of the *Mem. Amer. Acad. Arts* and *Sciences*. Boston and Cambridge, April 25, 1859. The theory is also summarized in Gager, C. Stuart. *Heredity and Evolution in Plants*. pp. 156–162. Philadelphia, 1920.

or spicy. The flowers are either perfect or unisexual; stamens 2–6 (rarely 8–10); pistil of 3 or more united carpels. The one-celled ovary is nearly or quite sessile. The tropical members include the Black Pepper, *Piper nigrum* (Fig. 394), a woody vine, usually dioecious, climbing by its roots, and native in the forests of the East Indies (Malabar and Travancore). It is cultivated throughout the old world tropics as a source of the black pepper of commerce, which is derived from the outer portion (exocarp)

Fig. 394.—At left, fruiting branch of Black Pepper (*Piper nigrum*). Portion of shoot with inflorescences; Terminal portion of inflorescence (enlarged). (After Wossildo.)

At right, the Cubeb (*Piper Cubeba*). *a*, cluster of fruit; *b*, staminate flower; *c*, pistillate flower in longitudinal section; *d*, fruit in longitudinal section. (After Berg and Schmidt.) Both from Strasburger, Noll, Schenck, and Schimper.

of the unripe fruit (drupes); the inner, stony portions of the fruit are the source of white pepper.

The officinal Cubeb is derived from the unripe fruit of *Piper cubeba*, a shrubby climber, native of Java and the Moluccas (Fig. 394). Betil leaves which, from early times, have been chewed by the natives of India and Indo-China, are the foliage of *Piper Betle* L., a perennial, dioecious, creeping plant, native in Java, and cutivated in India and Ceylon. The ornamental

Peperomias of our northern greenhouses also belong in the Pepper Family (Fig. 395).

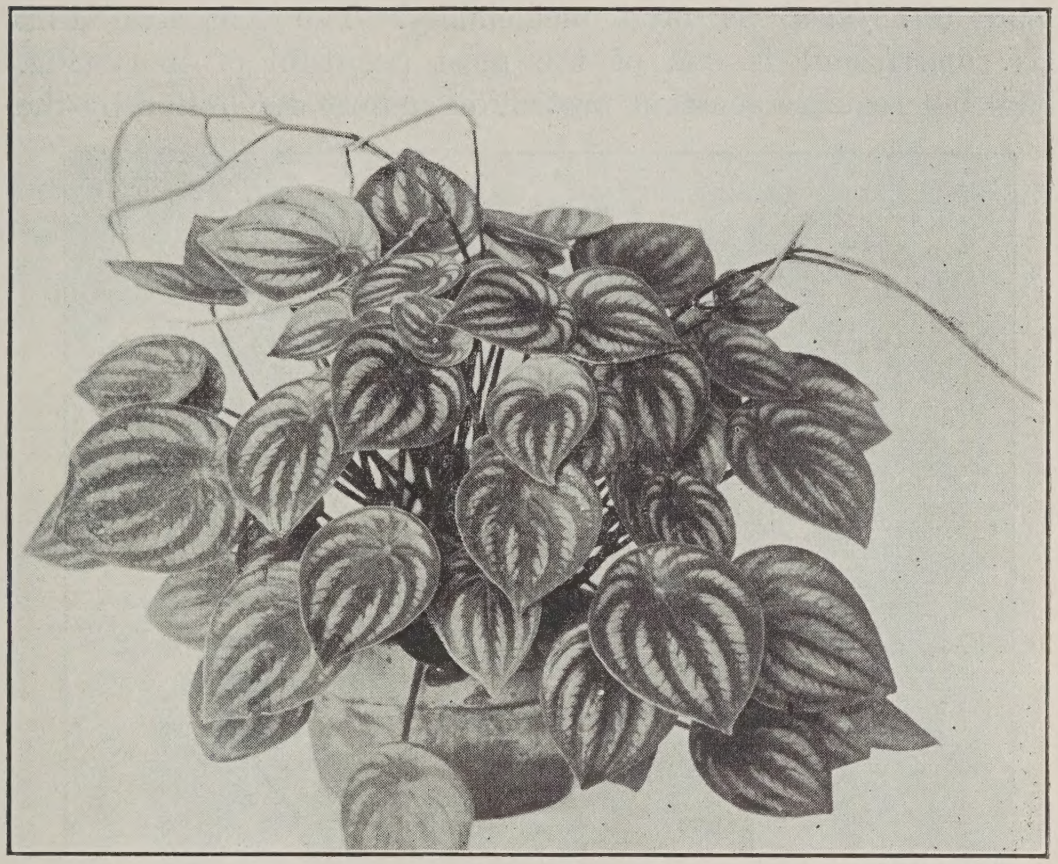


FIG. 395.—*Peperomia Saundersii* in flower.

ORDER, **Urticales**[1]

This order includes the Elms, the Nettles, and the Mulberries. The inconspicuous flowers possess a calyx but no corolla, and are never in catkins. Some botanists, placing the emphasis upon points of similarity, group all the genera in one family, the Urticaceae, with four or five subdivisions or "Tribes;" others, stressing the points of difference, make several family groups,—Ulmaceae, Moraceae, Cannabinaceae, and Urticaceae. The plants in the first two groups, as here defined, are trees.

[1] This order takes its name from the genus *Urtica*, the nettles. The generic name is derived from the Latin verb *urere*, to burn, and refers to the stinging character of the hairs of certain species, such as *U. dioica* and *U. urens*.

The Elm Family (*Ulmaceae*) are without latex and have seeds either winged (*Ulmus*), nut-like (*Zelkova*), or drupes (*Celtis*), but never achenes. The mucilaginous inner bark of the Slippery Elm (*U. fulva*) is used medicinally. The American Elm (*U. americana*) is one of the most beautiful of trees (Fig. 396) but requires constant protection against defoliation by the

FIG. 396.—Elm tree (*Ulmus americana*), showing deliquescent trunk.

gypsy moth, a very serious pest which defoliates nearly all native and introduced trees, as well as many kinds of garden crops and forage plants, and also by the elm tree beetle, which is one of the most persistent enemies of the elm.

MULBERRY FAMILY

The Mulberry Family (*Moraceae*) has latex, and the fruits are achenes, enveloped by the thickened, enlarged sepals, and grouped

to form a syncarp (Fig. 397), which is edible in the Mulberry and in the Bread Fruit (*Artocarpus*) of the South Sea islands. This family also includes the Paper Mulberry (*Broussonetia*), Osage Orange (*Maclura* Nuttall; *Toxylon* Rafinesque), and the Figs (*Ficus*).

The White Mulberry is of economic value because its fresh leaves form the necessary food for the larvae of the silkworm. The flowers of the mulberries are monoecious or dioecious, the 4-parted calyx with ovate lobes, stamens 4, ovary 2-celled, one cell disappearing as the fruit matures. The two thread-like styles

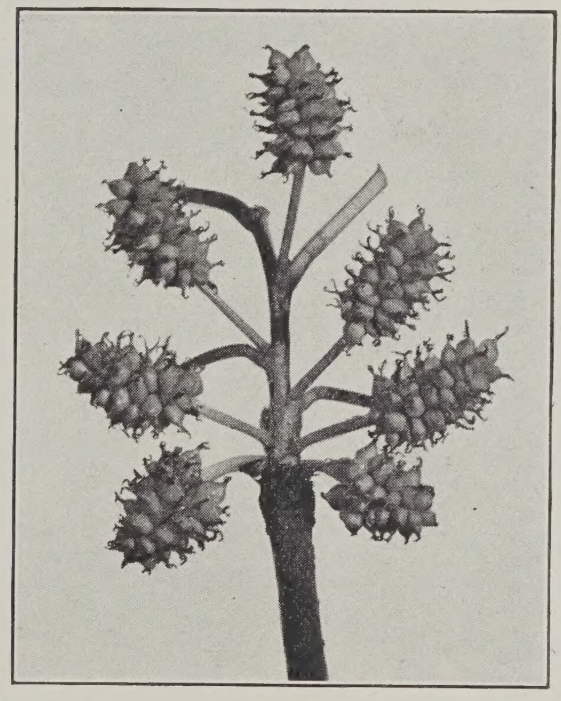


FIG. 397.—Fruit (syncarp) of red mulberry (*Morus rubra*).

are stigmatic along the inside. The ovary ripens into an *achene*, surrounded by the succulent calyx, the entire spike becoming an oblong multiple fruit, superficially resembling a blackberry, but only superficially, for the blackberry fruit consists of numerous small *drupelets* aggregated on a fleshy receptacle (*Cf.* p. 409).

The tropical genus *Ficus* includes the common "rubber plants" of our northern greenhouses and homes (*Ficus elastica* and others), the well-known "religious" fig-tree or Peepul tree (*F. religiosa*), the Creeping Fig (*F. pumila* L., =*F. repens* Hort.) used to cover stonework and walls in our northern conservatories, the famous

Banyan tree (*F. benghalensis* L.) of India and tropical Africa (Fig. 398), the Florida Strangling Figs (*F. aurea* Nutt., and *F. populnea* Willd.), and the edible Figs of commerce (*F. Carica* L.). The seeds of *Ficus aurea* are all but unique in that they require light in order to germinate,[1] and this appears to explain the fact that, while the plant grows rooted in the ground in open places, it commonly grows as an epiphyte in the dense hammocks of

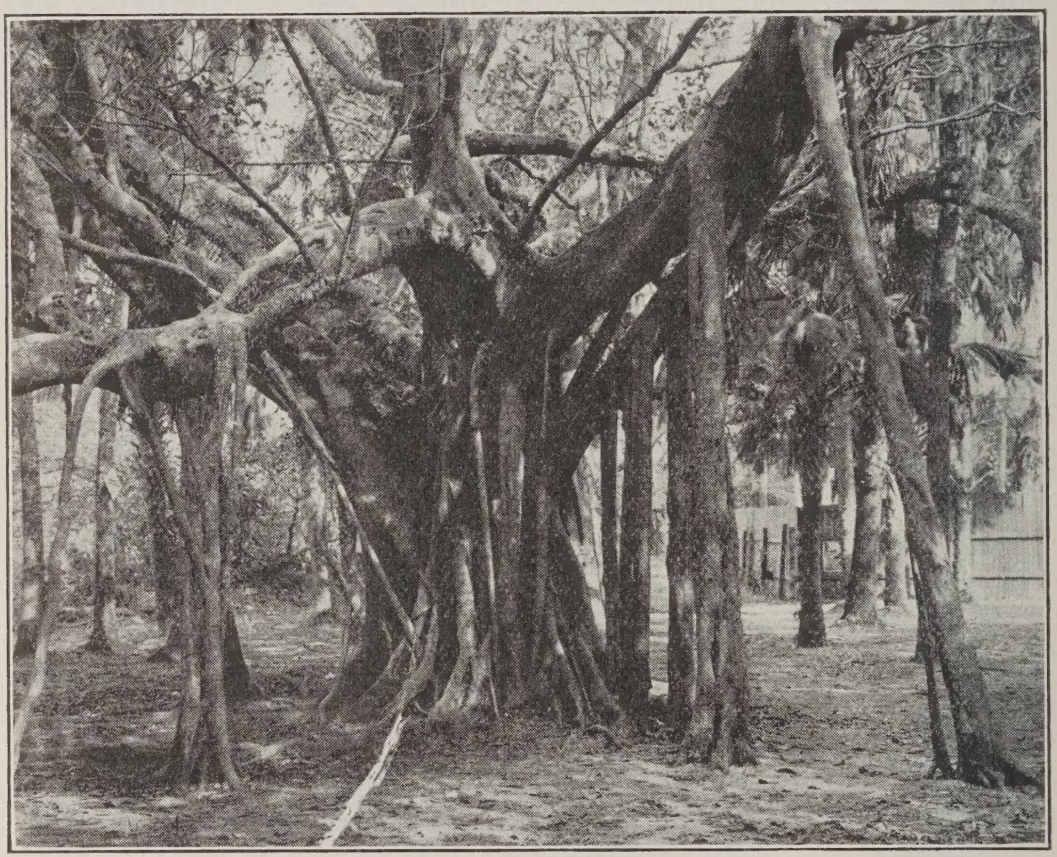


FIG. 398.—Banyan tree (*Ficus benghalensis*), showing main trunk and aerial roots that have grown downward from the branches into the soil.

Florida; there is not sufficient light on the ground in the hammocks to make germination possible.

EDIBLE FIGS

The edible figs of commerce are varieties of *Ficus Carica*. Botanically the fruit (called a *synconium*) is a hollow, pear-shaped receptacle with the flowers inserted on its inner surface (Fig. 399).

[1] Bessey, Ernst A. The Florida strangling figs. Missouri Bot. Gard. Ann. Rept. **19**: 25–33. 1908.

The cavity containing the flowers opens to the outside by a narrow passage or "eye," surrounded by a number of bracts; its diameter

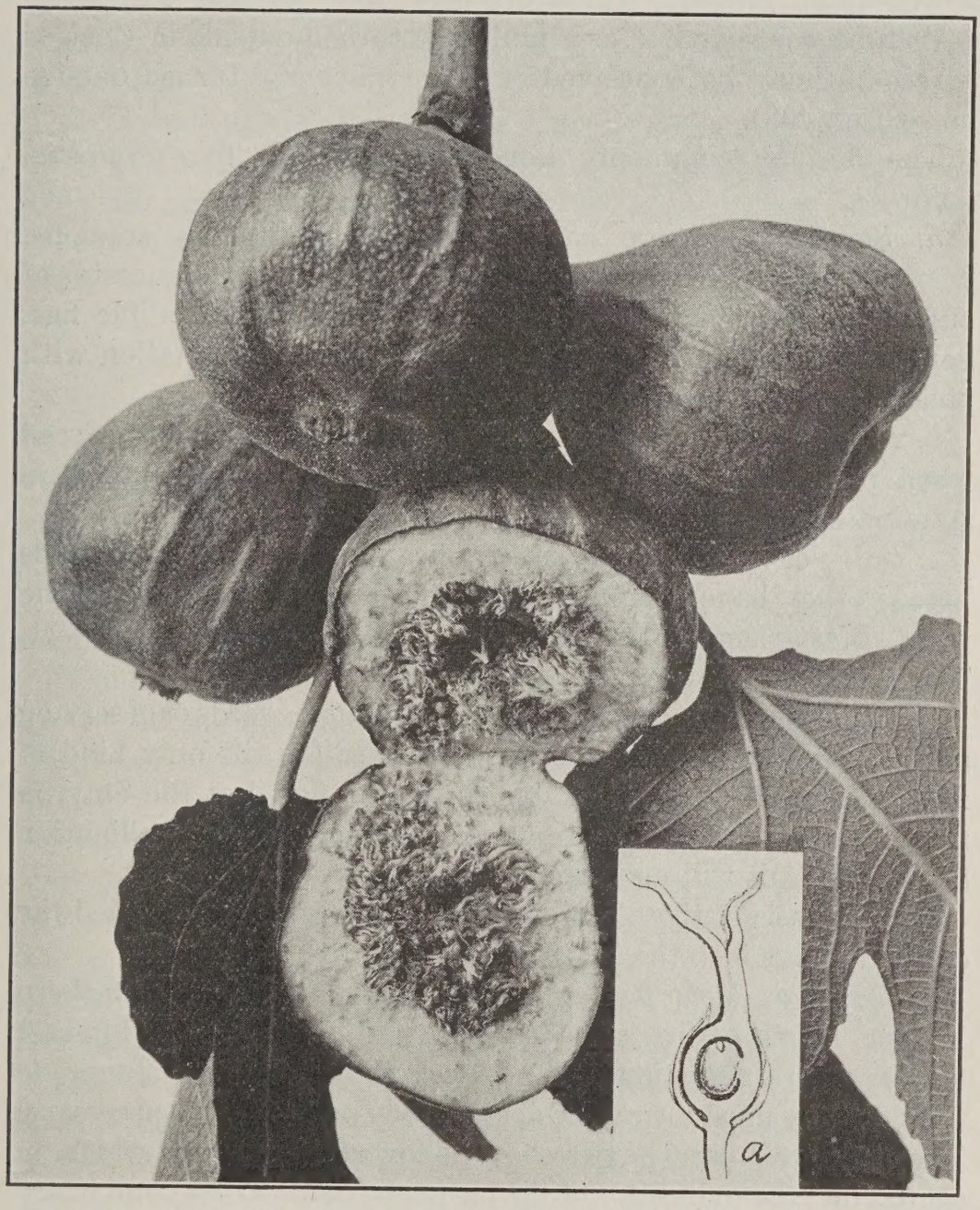


FIG. 399.—Profichi Caprifigs. The numerous flowers may be seen, inserted on the wall of the cavity of the fruit (synconium), shown in cross section. (Photo from George C. Roeding, Fresno, Calif.) *a*, insert, showing structure of pistillate flower, with ovary in median longitudinal section. (From Baillon.)

varies with the species and the stage of maturity. If the margin of a sunflower head were drawn up so as to form a sac with the

flowers inside we would have a fig-like inflorescence and "fruit." The fig inflorescence is really of the cymose type, with all the flower-stalks united. The fruit may also, as Asa Gray suggested, be conceived of as a mulberry turned outside in (just as a rose-hip may be conceived of as a strawberry turned outside in. *Cf.* p. 408).

The flowers, commonly imperfect, fall into four groups as follows:[1]

a. Staminate flowers, having four pollen-bearing stamens. These occur only in the wild "caprifig," the supposed ancestor of our cultivated figs, and in a very few varieties of edible figs. Sepals 2–6, or wanting; flowers nearly sessile. Pollination with pollen from the caprifig is called *caprification.*

b. Pistillate flowers, having one pistil which produces a seed when pollinated. Flowers short-stalked; sepals fewer than in staminate flowers, or wanting (Fig. 399).

c. Gall flowers, pistillate flowers incapable of producing seeds because they have been converted into galls by the sting of the wasp, *Blastophaga.* The gall contains the larva of the insect. These flowers occur only in the caprifig.

d. Mule flowers, incapable either of producing seeds or of serving as the breeding place of the wasp. These are the only kind of flowers in most varieties of our cultivated figs, but the Smyrna fig contains, also, pistillate flowers which require pollination before the fruit will mature.

On the basis of these flower differences Eisen has classified the cultivated figs into the following four groups:

1. *Caprifigs (goat figs or wild figs),* found wild in southern Europe, North Africa, and Western Asia. They bear all kinds of flowers except mule flowers, and, since they alone bear staminate flowers, they must always be grown when pollination is necessary. The pistillate flowers have a short hollow style, through which, in egg-laying, the ovipositor of the fig-wasp passes to the plant ovary where the insect's eggs are deposited.

2. *Smyrna figs,* grown in the Smyrna district of Asia Minor, bear only pistillate flowers, which differ from those of the caprifig

[1] Eisen, Gustav. Fig culture. U. S. Dept. Agr. Div. of Pomology. Bul. 5. 1897. Dr. Eisen is said to have been the first scientific man to recognize (about 1896) the importance or necessity of the wasp, *Blastophaga grossorum,* for cross pollination, at a time when others were skeptical.

in having a long, slender style. The ovary is one-celled. The flowers will not mature fruit unless they are pollinated with pollen from the caprifig. Early attempts to grow Smyrna figs in California were a total failure because the caprifig was not grown with them.

3. *Common Edible Figs.*—This is the fig commonly and successfully cultivated in California. There are probably as many as 600–800 varieties, of which over 400 varieties have been described. The fruit will mature without caprification, and the trees bear two crops a year—the early figs or "brebas," and the later "summer figs."

4. *San Pedro figs*, comprising a few dozen varieties and grown in California, Florida, and other southern states. The first crop (brebas) contains only mule flowers and therefore the fruit matures without pollination. The second crop always falls without maturing as the flowers are all pistillate and therefore the fruit cannot mature without pollination.

The fig tree is commonly propagated by cuttings, but may also be propagated by budding or grafting.

The caprifig in the Mediterranean region bears three crops of fruit—the spring crop or *profichi*, a second or *mammoni*, and a third the *mamme*, which remains on the trees all winter. The pollen of the mamme crop is only rarely viable. The larva of the fig-wasp winters over in the mamme, and in the spring lays its eggs in the ovaries of the modified pistillate flowers of the profichi. As soon as the fig wasps begin to emerge, the caprifigs (*profichi*) are gathered and placed in wire baskets or otherwise distributed in the branches of the Smyrna fig trees. This is done in early morning for the wasps come out only in the forenoon. This is repeated every three or four days for two or three weeks. The staminate flowers of the profichi inflorescence are borne above the pistillate flowers, so that as the imago (mature flying insect) emerges from the profichi she becomes covered with the abundant yellow pollen. Flying to the Smyrna figs she enters through the "eye" into the receptacle. As the insect moves about among the pistillate flowers the stigmas become well pollinated.

There are two crops of Smyrna figs—*brebas* and *higos*. The brebas fail to mature, dropping off early because their flowers do not get pollinated on account of the absence of viable pollen in

the mamme crop of caprifigs. The higos appear at the right time to receive pollen from the profichis, and become the figs of commerce.

The success of Smyrna fig culture in the United States began about 1899, when W. T. Swingle, of the U. S. Department of Agriculture, began sending from Europe the winter generation (mamme) of caprifig containing the fig-wasp, instead of the profichi generation, as had hitherto been done. In a similar manner fig culture failed in South Africa and Australia until the fig-wasp was introduced.

FIG. 400.—Hemp (*Cannabis sativa*). (After Britton and Brown.)

The Hop or Hemp Family (*Cannabinaceae*) are erect or climbing herbs, with dioecious flowers, the calyx having but one (persistent) sepal (Fig. 400). The blades of the alternate or opposite leaves are palmately divided into 3–5 narrow segments. The fruit is a glandular achene. The principal genera are the hemp and the hop. The Hemp (*Cannabis sativa*) is a tall annual, the tough fibers of the inner bark being used to make cordage, tow, binder-twine, and other articles (Fig. 401). In the United States hemp culture is largely confined to a few counties of central Kentucky.

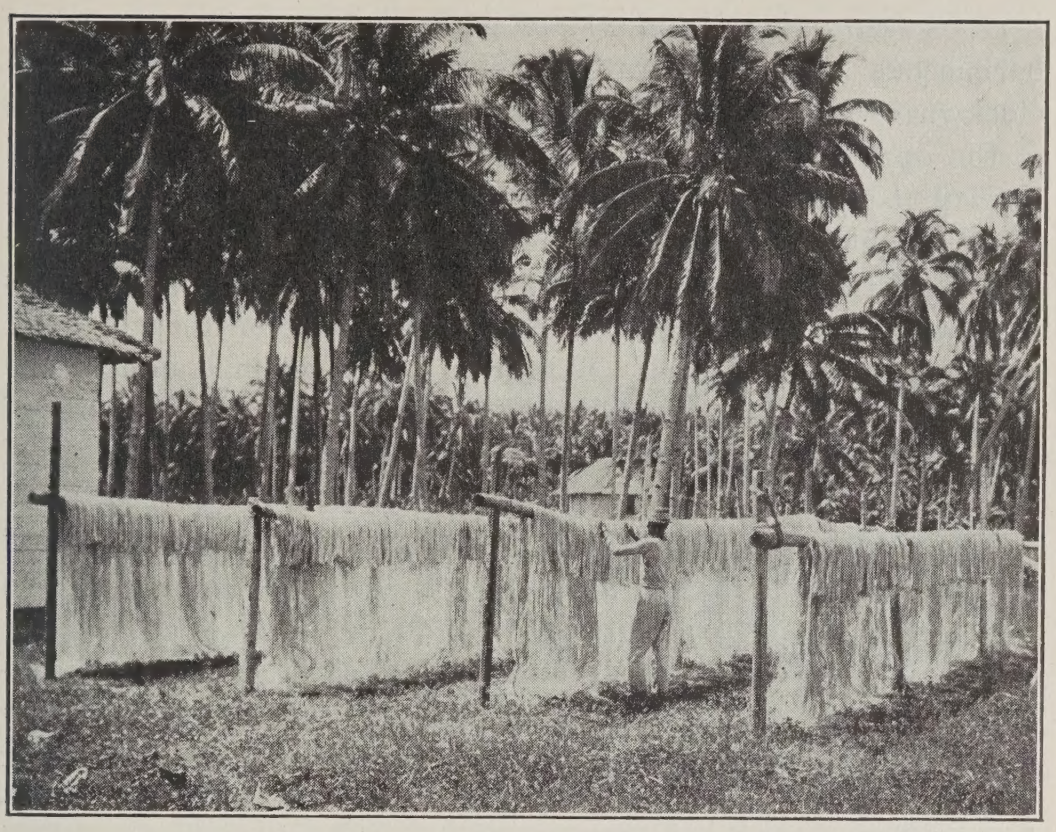


FIG. 401.—Drying hemp fiber. (Photo from Bureau of Science, Manila.)

FIG. 402.—Hop (*Humulus Lupulus*). (After Britton and Brown.)

Hops (*Humulus Lupulus*) are perennial, coarsely pubescent, herbaceous vines, prostrate or climbing by twining counter-clockwise (*i.e.*, left-handed) about the support. The blades of the opposite leaves are 3–7 lobed, with serrate margins, and persistent stipules. The flowers are dioecious, the staminate in loose panicles, the pistillate on short spikes or catkins. The leaf-like bracts are imbricated, and the inflorescence develops into what may be called a membranaceous cone, each bract subtending two achenes. This fruit is known in commerce as "hops." The plant is one of the most widely cultivated of all plants, being grown in nearly every civilized country in both hemispheres (Fig. 402).

FIG. 403.—Buckwheat (*Fagopyrum esculentum*). (After Britton and Brown.)

The Nettle Family (Urticaceae) comprise chiefly weeds, including the Stinging Nettle (*Urtica dioica*), Richwood or Clearweed (*Pilea pumila*), and others.

ORDER, Polygonales

This order contains only one family, the *Polygonaceae*, or buckwheat family. The botanical name of buckwheat is *Fagopyrum*, meaning "beechwheat," from the Greek *fagus*, (φαγός) meaning *beech*, and *pyrus* (πυρός) meaning *wheat*. The German word for beech is *Buche*, whence the English form, buckwheat. The name refers to the resemblance of the seeds (achenes) to small beechnuts (Fig. 403). After cultivation in a field, buckwheat persists for a long time as a weed, and escapes to adjacent waste places.

In addition to the valuable buckwheat, the Polygonaceae contain the weedy docks (*Rumex* sp.), the sorrels of the same genus, the knotweeds (*Polygonum*), and the common "pie-plant," or rhubarb (*Rheum rhaponticum*), whose acid leaf-stalks are used as a filling for pies, and for the making of wine. Other

species of *Rheum* are planted for the ornamental character of their foliage.

OTHER ORDERS

The *Salicales* are dioecious trees or shrubs with the imperfect flowers born in catkins (Figs. 404 and 405). Sepals and petals are wanting, the leaves are simple, the fruit is a many-seeded capsule, and the seeds have a tuft of hairs at one end. The

FIG. 404.—Glaucous willow (*Salix discolor*). Staminate inflorescences. (Photo by L. W. Brownell.)

one family in the order, the Willow Family (*Salicaceae*), contains two genera, *Populus* (Poplar) and *Salix* (Willow), comprising altogether about 200 species. Although the willow flowers have no corolla they are pollinated, not by wind, but by insects, and for this and other reasons it is an unsettled question whether the simple structure of the flowers is a truly primitive character, or whether it is to be considered as resulting from reduction in the course of evolution from ancestors that had a more highly devel-

oped flower. Salicylic acid, as its name implies, is derived from the glucoside, *salicin*, found in the leaves and bark of several species of willows and poplar, oil of wintergreen, and other sources. This is one of the ingredients of "aspirin" (which is the mono-acetic acid-ester of salicylic acid).

The *Myricales* contain one family, the Sweet Gale Family (*Myricaceae*) and, according to some authors (following Linnaeus), only one genus, *Myrica* of about 35 species, including the Sweet

FIG. 405.—Glaucous willow (*Salix discolor*). Pistillate inflorescences. (Photo by L. W. Brownell.)

Gale (*Myrica Gale*), the Wax Myrtle (*M. cerifera*), the well-known Bayberry (*M. carolinensis*), and the Sweet Fern (*M. asplenifolia*). According to other systematists (following Aiton[1]), the Sweet

[1] WILLIAM AITON. b. Hamilton, Scotland, 1731; d. Kew, England, 1793. He was a pupil of Philip Miller at the Chelsea Physic Garden, and in 1759 was engaged by Princess Augusta as one of the gardeners at Kew House, already famous for its collection of rare plants. Under her instructions Aiton established at Kew a physic garden, modeled after that at Chelsea, and thus laid the foundations for the modern Royal Botanic Gardens, Kew. His "*Hortus Kewensis*, or a Catalog of the plants cultivated in the royal botanic garden at Kew," was published in 1793.

Fern is placed in a separate genus *Comptonia*, with the specific name, *C. asplenifolia*.

The *Leitneriales* has but one family (*Leitneriaceae*), one genus (*Leitneria*), and one species (*L. floridana*). The wood is one of the lightest known, having a specific gravity of only 0.207 with water taken as a unit. This is lighter than Balsa wood, which has a specific gravity of 0.250.

The *Juglandales* comprises the Walnut Family (*Juglandaceae*), containing the Black Walnut (*Juglans nigra*) and the white walnut or Butternut (*J. cinerea*), and the economically important "English" Walnut (*Juglans regia*). In colonial days and after, in the United States, the oil of the cotyledons of the butternut was often used to lubricate the wooden works of the tall "grandfather's clocks."

Massey has recently determined that the roots of Butternut and especially of Black Walnut secrete a substance which is toxic to various crop plants, such as alfalfa, tomato, and potato. The toxic substance is not generally distributed in the soil around the walnut trees, but is localized in the vicinity of the walnut roots, and roots of affected plants were always found in close contact with the walnut roots.[1]

Another important genus of the north temperate zone is *Carya* or *Hicoria*, containing the pecan and the hickory nut. In this family is included also the Circassian walnut (*Pterocarya*) of the Caucasus region.

The *Fagales* include the Birch Family (*Betulaceae*) and the Beeches (*Fagaceae*), the former comprising the Hornbeams (*Carpinus*), Ironwood (*Ostrya*), Hazelnut (*Corylus*), Birches (*Betula*), and Alders (*Alnus*). In the latter family are found the Beechnut (*Fagus*), Chestnut (*Castanea*), and the numerous species of Oaks (*Quercus*).

ORDER, Chenopodiales

This order includes several families of herbaceous plants, nearly all apetalous, with central placentation and curved embryo in the seed. The principal families are the Goosefoot Family

[1] Massey, A. B. Antagonism of the walnuts (*Juglans nigra* L. and *J. cinerea* L.) in certain plant associations. Phytopathology **15**: 773–784. Dec., 1925.

(*Chenopodiaceae*), the Amaranths (*Amarantaceae*), Pokeweeds (*Phytolaccaceae*), Purslanes (*Portulacaceae*), the Pinks (*Caryophyllaceae*), and other families of less economic importance. Some authorities place the last two families in another order, the Caryophyllales, distinguished from the Chenopodiales (in the more restricted sense) by having opposite (instead of alternate) leaves, several or many (instead of one) seeds, and otherwise. The order includes only herbs with perfect flowers, the calyx usually present, the corolla sometimes wanting (Fig. 406). The Goosefoot Family contains the genus *Chenopodium* (Lamb's Quarter or Goosefoot) with numerous (frequently weedy) species; *Kochia*, often cultivated for its attractive autumn foliage, and other genera less important economically.

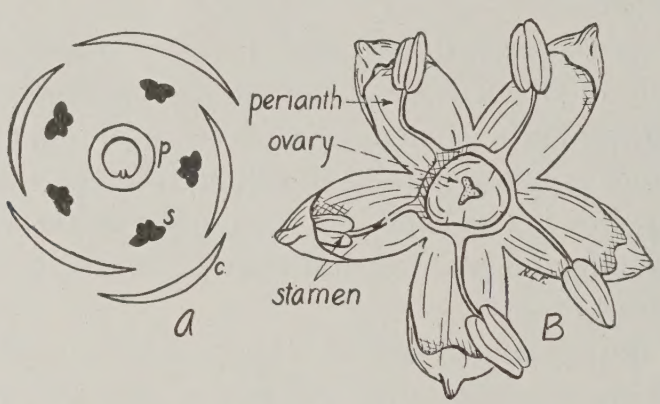


FIG. 406.—Beet (*Beta vulgaris*). *A*, floral diagram; B, flower, face view. (A, after Bessey; B, after Robbins.)

The Goosefoot Family (*Chenopodiaceae*) includes the plant *Beta vulgaris*, from which have arisen horticultural varieties of two types—those with large succulent leaves, but with small fibrous roots, and those characterized by thick, fleshy roots. The former comprise the Swiss Chard or Sea-Kale Chard, known also as *Beta vulgaris Cicla*. There are two sub-groups of this plant: 1. Those in which the large leaves are used like spinach (Fig. 407). One form of this sub-group has a thick leaf-stalk and midrib, often cooked by itself, like asparagus. By some the term chard[1] is confined to this latter type, the whole group being

[1] The name chard is derived through the French from the Latin *carduus*, a thistle or artichoke. The leaves of one of the artichokes are edible and the name chard was transferred, in common usage, from one plant to the other of similar character in this respect.

called "leaf-beets." 2. Those with variegated leaves, and grown for ornament (*Beta vulgaris cruenta*).

The garden beet, whose fleshy root is much prized as a table vegetable, is known to have been grown by the ancient Greeks and Romans several centuries before Christ. The Romans

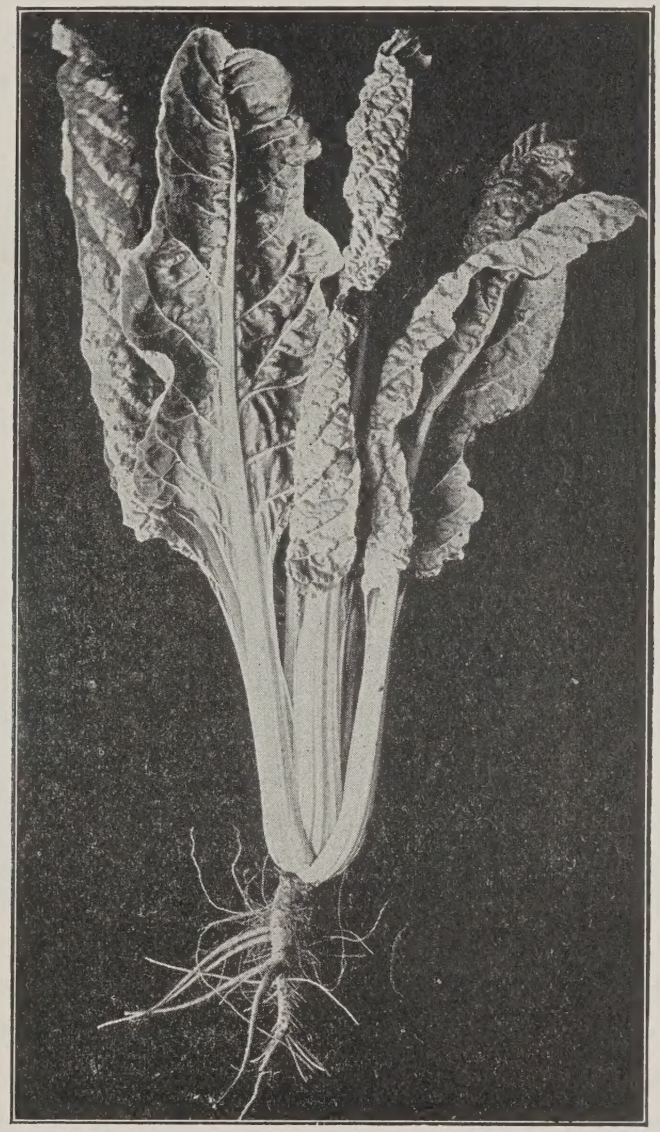


FIG. 407.—Swiss Chard (*Beta vulgaris Cicla*). (After Robbins.)

called it *beta*. The plant is an annual or biennial, with entire leaves, and perfect flowers with the 5-lobed perianth adhering to the ovary and becoming hard or corky in the fruit. The 5 stamens are borne on a fleshy ring. The so-called "seed" is composed of two closely adhering ovaries.

The wild *Beta vulgaris* is a perennial, often decumbent plant, freely branching, and gowing wild on the coasts of Europe. It is common on the shores of Italy, and seems to prefer localities near the sea. In fact, Linnaeus, at first, called it *Beta maritima*. The branching form has been called *B. patula*. Plants raised by de Vries from seeds of this form varied greatly from forms with thin, woody roots to nearly typical sugar beets. Several students of this question consider *B. patula* as the most probable wild ancestor of our garden and sugar-beets.

The beet is of historical interest in plant breeding, for this was the plant with which Louis Vilmorin[1] worked. He is said to have been the first systematically to apply to plants the principle of selection for race improvement, although this had been done for animals long before Vilmorin. He applied the principle to increase the sugar content of beets, and succeeded in increasing the sugar from 7% to 21%. An extreme of as much as 23% has been obtained (26% has been reported).

Spinach (*Spinacia oleracea*), an annual herb whose arrow-shaped "root-leaves" form one of the most important "greens," is also in the Goosefoot Family, and is thought to be native in Southwestern Asia. The plant is an annual, and late in the season produces a branching flower-stalk, which bears small clusters of dioecious flowers. As in the beet, the calyx hardens in the fruit, enclosing the achene, and in one species it becomes spiny, hence both the common and generic names, from the Latin word, *spina* (a thorn or prickle).

The *Amarantaceae* contains one of the commonest of weeds, the Pigweeds (various species of *Amarantus*), frequent throughout the northern United States, except in the higher latitudes. The Greek word "amarantos" (ἀμάραντος) means *unfading*, for the dry calyx and the bracts do not wither.

The Pokeweed Family (*Phytolaccaceae*), is of only minor economic importance.

[1] Pierre Louis Francois Levêque Vilmorin. One of the most famous of plant breeders, was born in Paris in 1816, and died at Verrières (near Paris) in 1860. Inheriting a commercial seed business that had been in his family nearly 200 years, he devoted himself to the study of plant breeding with a view to improving the quality and yield of crop plants. Nearly all the plants of French agriculture were studied and improved by him, including beets, cereals, potato, madder, flowering plants, and many others.

In the Purslane Family (*Portulacaceae*) is the genus *Portulaca*, whose flowers open only in sunshine. *Portulaca grandiflora*, with flowers of many colors, is a good carpet-plant and may be successfully used in sandy yards around cottages by the seashore, where it is difficult or impossible to establish a lawn. Pusley (*P. oleracea*) is a troublesome trailing weed, common in gardens, and used in some places as "greens."

The plants of the *Caryophyllaceae*, or Pink Family, are herbs with opposite, entire leaves, and the flowers symmetrical, with

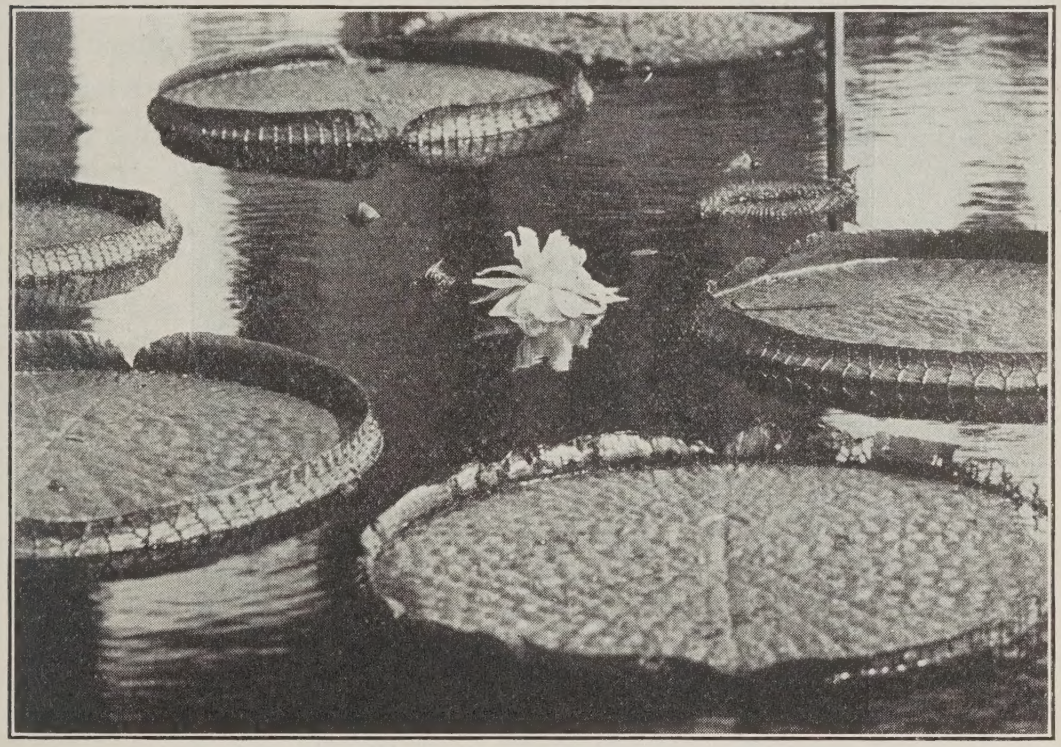


FIG. 408.—*Victoria Cruziana* in flower.

the parts in fours or fives, with or without petals. The stamens are usually 8 or 10, and the fruit is a capsule with one or many seeds with endosperm. Here belong the Sand Spurrey (*Spergularia*) and Sandwort (*Arenaria*) of the seashore, the Mouse-ear Chickweed (*Cerastium*), the Corn-cockle (*Agrostemma*) of our grain fields, Campion (*Lychnis*), Catchfly (*Silene*), Bouncing Bet or Soapwort (*Saponaria*), *Gypsophila*, and *Dianthus*, comprising the wild and the cultivated pinks—Sweet William (*Dianthus barbatus*), and Carnation (*Dianthus Caryophyllus*). The carnation has been cultivated for 2000 years or more. Its specific

name is due to the fact that it has the odor of cloves (*Caryophyllus aromaticus*). There are innumerable horticultural varieties of carnation, with various odors and shades of color.

The juice of the Bouncing Bet, or Soapwort (*Saponaria officinalis*), readily makes a suds with water, and is the basis of the foam of so-called "soda water."

ORDER, Ranales

This order, like so many of the others, is named from one of its chief families—the Crowfoot Family (*Ranunculaceae*). By

FIG. 409.—Flower of magnolia. (Cf. Fig. 410.)

some botanists the order is called *Ranunculales*. It comprises aquatic and marsh plants, herbs, shrubs, and trees. Both calyx and corolla are usually present and are of separate sepals and petals. The superior ovaries are free from the calyx, the one-to-many carpels are usually separate, and the hypogynous stamens are more numerous than the sepals.

WATER LILY FAMILY

The Water Lily Family (*Nymphaeaceae*) includes the Fanwort or Fish-grass (*Cabomba*), so commonly used in fresh water aquaria, the Yellow Waterlilies (*Nuphar*), the White Waterlilies

(*Nymphaea*), the American and the Indian Lotus (*Nelumbo lutea* and *N. nucifera*), and the Watershield (*Brasenia*). Tropical forms of Nymphaea, with beautiful shades of pink, blue, and red, are grown in botanic gardens and parks of the north temperate zone in artificially heated pools. A common, though not universal difference between tropical and temperate forms is that the former have pointed petals, while the latter do not. Here belongs the famous *Victoria regia*, of equatorial South America, and *V. Cruziana*, of Paraguay (known also as *Victoria regia Trickeri*). This plant has one of the largest flowers known, and the floating leaves, with upturned margins (Fig. 408), will support a small child if a thin board is laid over the blade so as to distribute the weight. The respiration of the flower is so vigorous that temperature fluctuations of as much as 15° C. have been observed within the perianth. The seeds of some water lilies contain gas bubbles which buoy them up, and thus facilitate their distribution by currents of water.

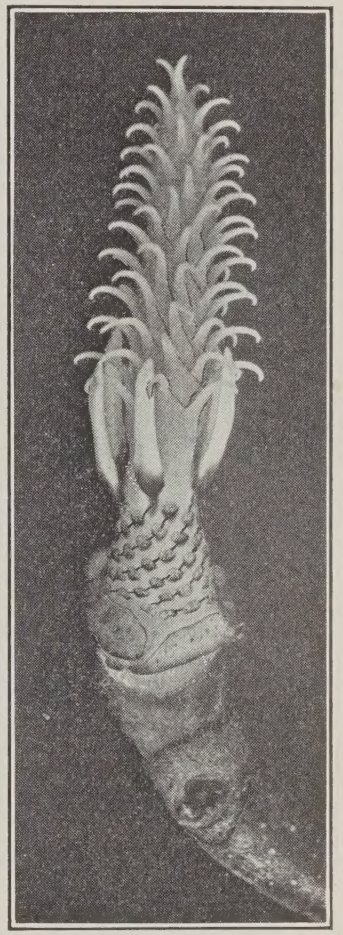


FIG. 410.—Magnolia. Flower with perianth removed, showing the compound pistil, and four of the stamens. Most of the stamens have been removed. Note their spiral arrangement as shown by the scars at the points of attachment. (Cf. Fig. 409.)

MAGNOLIA FAMILY

The Magnolia family shows many primitive characters, such as having all the parts of the flower separate, a spiral arrangement of the stamens and pistils (Figs. 409 and 410), and no clear distinction between sepals and petals. It suggests, in some ways, the "floral" structure of the fossil Cycad, *Cycadeoidea*.

The family contains about ten genera and seventy species, represented in the north temperate zone only by various species of *Magnolia*, and by the Tuliptree (*Liriodendron Tulipifera*). Magnolias and tuliptrees are largely planted as ornamental trees, and the wood of the tuliptree (known commercially as "white

wood" and "yellow poplar") has a rather extensive commercial use. The trunks of both trees are excurrent, and the tulip-tree attains a maximum height of about 200 feet.

CUSTARD-APPLE FAMILY

The Custard-apple Family (*Anonaceae*) is confined largely to the tropics. It includes the Custard-apple (*Anona reticulata*), Sugar-apple or Sweet-sop (*A. squamosa* (Fig. 411), Cherimoya

FIG. 411.—Fruit of a hybrid *Anona Squamosa* (Sugar-apple or Sweet-sop). (U. S. Dept. Agr.)

(*A. Cherimolia*), Sour-sop (*A. muricata*), and other edible species of the tropics and sub-tropics; also the North American Papaw (*Asimina triloba*). The latter should not be confused with the Papaya of the Caricaceae, also, sometimes, called Papaw (p. 687).

NUTMEG FAMILY

Related to the Anonaceae are the *Myristicaceae*, a family of woody, evergreen, dioecious plants. There is only one

genus, *Myristica*, with some 80 species distributed in tropical Asia, Madagascar, tropical Australia, Guinea, and South America. The fruit is a berry and the seeds have a fleshy aril (p. 356). *Myristica fragrans* is the nutmeg of commerce, and the aril of the nutmeg seed is *mace* (Figs. 412 and 252).

FIG. 412.—Nutmeg (*Myristica fragrans*); leafy branch, fruit, and seed with aril (mace). × ½. Cf. Fig. 252. (After Maxon. Photo from Castleton Gardens, Kingston, Jamaica.)

CROWFOOT FAMILY

The largest family of the order is the Crowfoot Family (*Ranunculaceae*), comprising about 35 genera and about 1000 species found in all parts of the world. There are some 30 species, more or less, in the Northeastern United States. Among the genera grown commercially for their horticultural or medicinal value are the Windflowers (*Anemone*), Globeflower (*Trollius*) (Fig. 349), Virgin's Bower (*Clematis*), Goldthread (*Coptis*), Hellebore

(*Helleborus*), Columbine (*Aquilegia*) with numerous horticultural forms, Larkspur (*Delphinium*) with many horticultural varieties, Aconite or Monkshood (*Aconitum*), and the Peony (*Paeonia*), with a large number of named horticultural varieties.

In contrast to many other genera of this family the peony has several ovules in each carpel (Fig. 415) (several genera have a one-seeded, indehiscent achene), showy petals (many genera have no petals), and a concave instead of a convex receptacle. The flowers are complete and regular. *Paeonia albiflora* (Fig. 416)

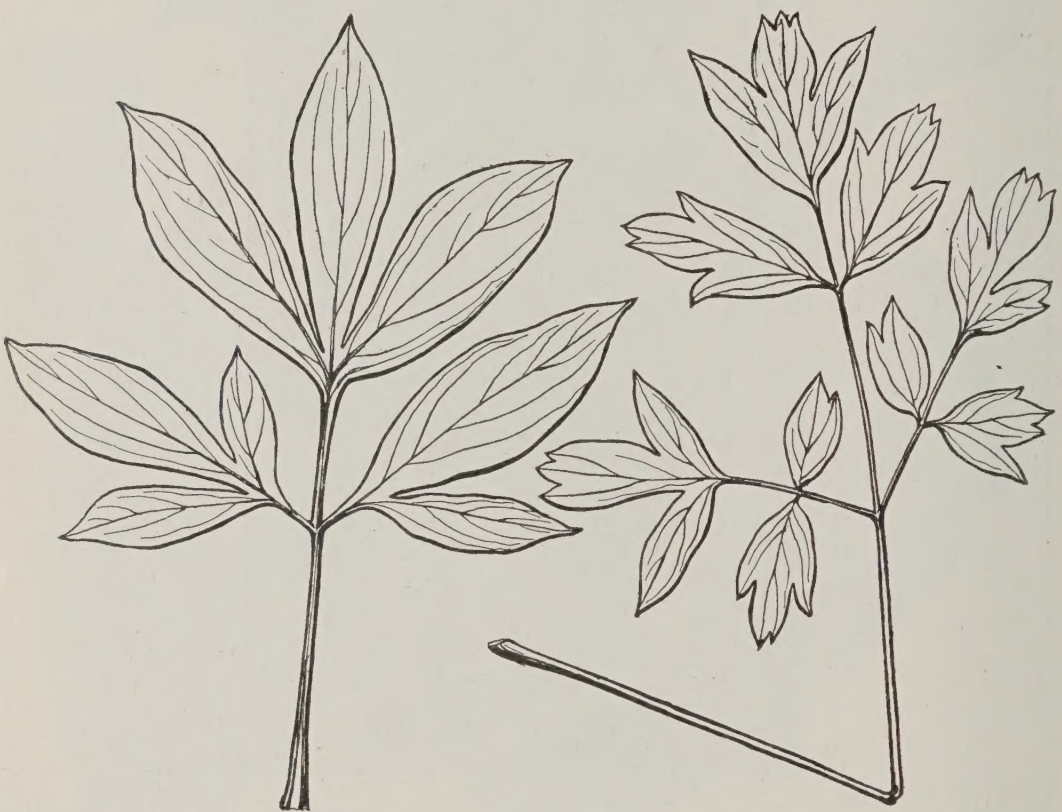


FIG. 413.—A, leaf of a herbaceous peony; B, leaf of a tree peony.

is one of the most primitive in flower-structure, with five sepals imbricated in the bud, and petals (often five) also imbricated in the bud. The numerous stamens are inserted on a spiral. The gynoecium is composed of a varying number of free carpels, each of which has a longitudinal groove bearing stigmatic papillae. In contrast to most of the Ranunculaceae, the peony seed has an aril, fleshy in character, and formed by the dilation of the funiculus surrounding the hilum. In one section of the genus there are two corollas of three petals each, the inner alternate with the

outer (*e.g.*, *P. Wittmaniana*). The peonies all have perennial roots, but fall naturally into two groups, namely, *Tree Peonies*, which have perennial (*i.e.*, woody) stems, and *Herbaceous Peonies*, which have herbaceous stems, dying back to the ground each winter. These two groups are also distinguished by other structural differences, and have been derived from different wild species.[1]

Tree Peonies.—The twice pinnately compound leaves are strikingly different from those of the herbaceous peony, which are

FIG. 414.—Leaves of a herbaceous peony, showing gradual transition from a pinnate foliage leaf (*a–d*) to single hypsophylls or bracts (*e–f*), a bud scale (g), and finally to a sepal (*h*). All of these leaves were borne on the same branch, *a*, at the bottom, and *h* at the top. *a–d*, reduced about ⅓; *e–h*. × 2.

only once compound. Also in contrast to the herbaceous species, the leaves of the tree peonies continue compound up to and including the last leaf immediately below the flower. The leaf blade is thicker and of coarser texture, and silvery underneath. The leaf stalk is not winged between the leaflets as in the case of the herbaceous type (Fig. 413). The buds are also larger and flatter than those of the herbaceous kind, and are pointed at the center. The flowers are both single and double, depending upon the variety.

[1] For the paragraphs on the peony I have drawn freely on J. Eliot Coti. The Peony, Cornell Univ. Agr. Exp. Sta. Bul. 259. Nov. 1908, and Mrs. Edward Harding. The book of the peony. Philadelphia and London, 1917.

The tree type was distinguished from the herbaceous by the Chinese as early as 536 A.D., the tree peonies being called Mow Tan, meaning "male scarlet flower," hence the specific name,

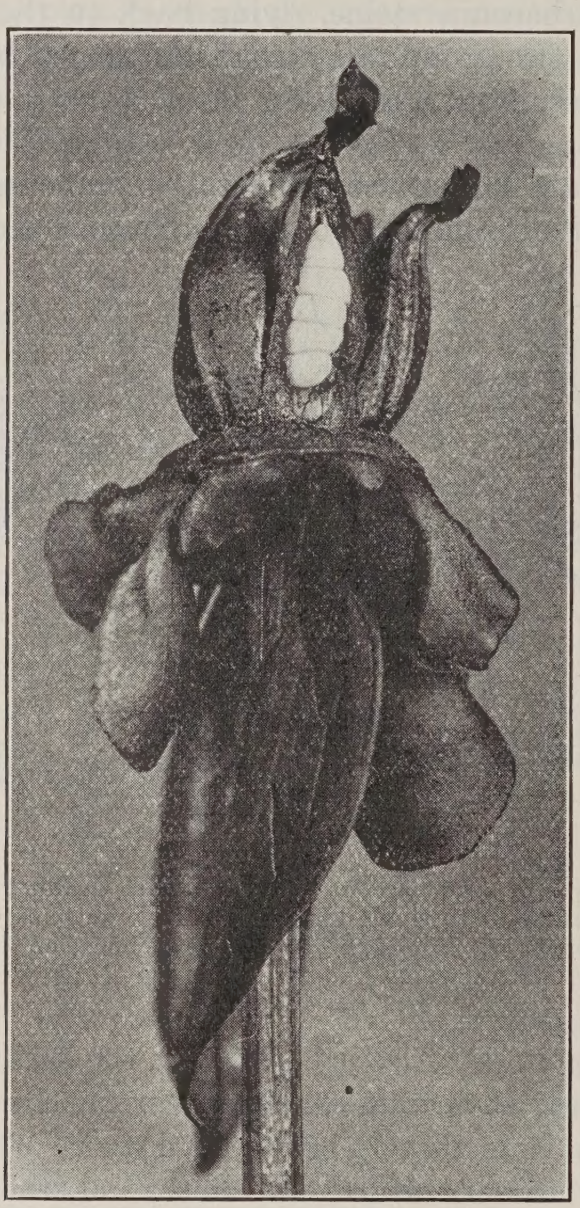


FIG. 415.—Carpels and hypsophylls of a peony flower after the petals and stamens have fallen away. One of the 5 carpels is shown with a portion of its wall removed, disclosing 5 ovules that are ripening into seeds.

Paeonia Moutan Sims, now called *Paeonia suffruticosa.* Ancient Chinese writers agree that the native home of the *moutan* is in the district of Hang Chung in the eastern part of the province of See Chuen and the adjacent southern part of Shen Se. Previous to

about 600 A.D. the plant was grown chiefly for the supposed medicinal properties of its roots, but from that date it began to be cultivated as an ornamental plant in gardens. The plant was introduced into England by Sir Joseph Banks[1] in 1794. Between two and three hundred varieties are cultivated in China.

Mrs. Harding mentions a tree peony in the garden of E. Taylor, Diss, Norfolk, England, which, in 1904, at the age of 80

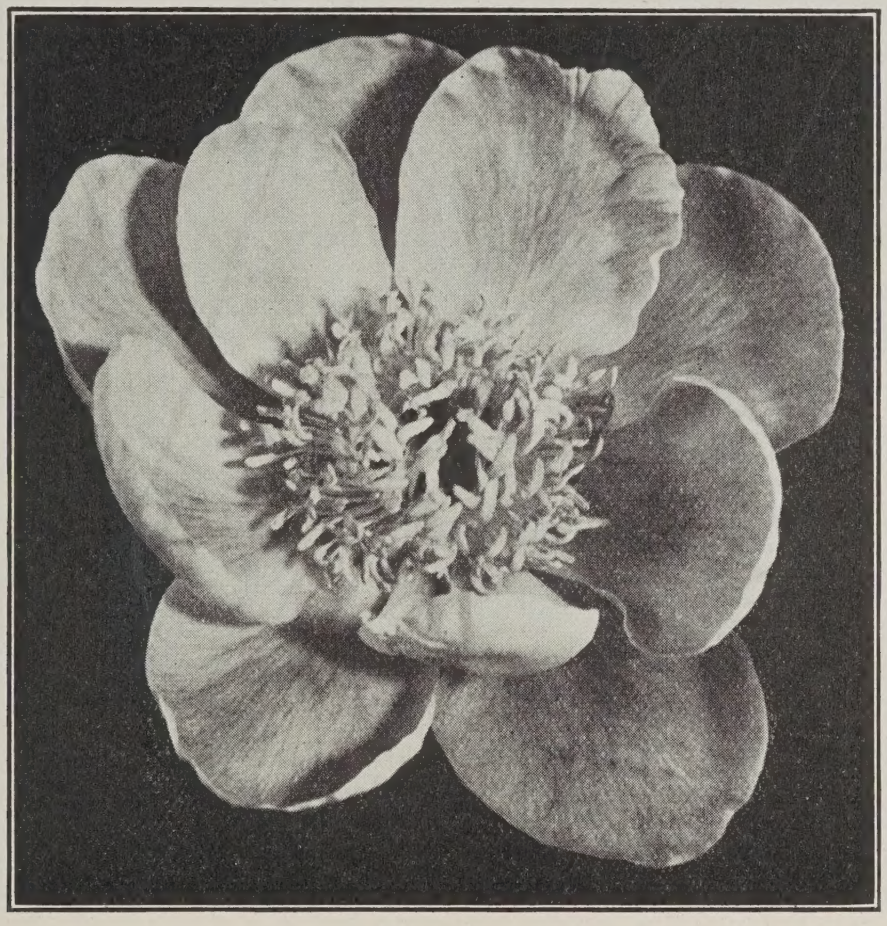


FIG. 416.—Flower of *Paeonia albiflora* with ten petals. Semi-double type.

years, produced 400 flowers from 8 to 9 inches in diameter. The tree peony was introduced into America probably about 1820.

[1] SIR JOSEPH BANKS (1743–1820) was an English naturalist born in London. Through him botanical lectures were first introduced into Oxford University. He made extensive botanical explorations and collections with Capt. Cook and others, and in 1778 became president of the Royal Society. His books and herbarium were bequeathed to the British Museum. The genus *Banksia*, of the Proteaceae, and several species of plants are named from him.

Herbaceous Peonies.—The leaves of the herbaceous peonies grow increasingly simpler from the lower to the upper part of the stem, until they are reduced to a simple bractlike leaf just below the flower (Fig. 414). As early as 536 a Chinese writer classified the herbaceous peonies into two groups—white and red. The plant was generally cultivated throughout China by the early

FIG. 417.—Flower of herbaceous peony, "Gen. Bertrand," illustrating the Japanese type of double flower, the narrow inner petaloids being metamorphosed stamens (staminodes).

part of the eleventh century, and as many as 30 varieties were offered by Chinese nurserymen as early as 1596.

This is the plant which Homer tells us was used by the Greek physician Paeon to cure Pluto of an illness, and the genus is named in honor of Paeon. The plant is now considered of value only for the beauty of its flowers.

Doubling of the flowers results in two ways, (*a*) from the replacement of the normal stamens by *staminodes*, which appear to result from the abortion of the anthers and the flattening of the filaments so that they resemble narrow petals (Fig. 417); (*b*) the replacement of the carpels by *carpelodes*—organs that resemble the petals more nearly than do the staminodes. Both staminodes

FIG. 418.—Flower of herbaceous peony, "Dr. Bretonneau," illustrating the semi-rose type of double flower, the inner petaloids being metamorphosed carpels (carpelodes). Note the unmetamorphosed stamens surrounding the carpelodes.

and carpelodes are referred to by the common name, *petaloids*. In some types there are secondary as well as primary petaloids (Fig. 418).

When the primary petals or *guards* are longer, larger, and otherwise quite distinct from the petaloids the flower is said to be *differentiated*, as in the Japanese type; otherwise the flower is undifferentiated, as in the rose type.

Paeonia is what botanists call a "critical" genus, there being no general agreement as to the eighteen to twenty-five species within the genus.

The Barberry Family (*Berberidaceae*) has about 10 genera and over 100 species in the north temperate and south temperate zones, and a few tropical species. There are usually 6 sepals and 6 petals (rarely 2 or 4), and the stamens are as many as the petals. The pistil is composed of a single carpel, and the fruit is a berry or a pod. The well-known Mayapple or Mandrake (*Podophyllum peltatum*) of the United States belongs here, as do also the Twinleaf (*Jeffersonia diphylla*), the Umbrella-leaf (*Diphylleia cymosa*), the Blue Cohosh (*Caulophyllum thalictroides*), and the Barberry (*Berberis*), so named by Tournefort before the time of Linnaeus, from the Arabic name of the fruit, *Berberys*.

Various species of Barberry are extensively used as hedges, both clipped and unclipped, and otherwise for decorative planting. The common barberry (*B. vulgaris*), the Japanese barberry (*B. Thunbergii*), and others have brilliant fall foliage, and the latter retains its bright red fruits until spring. A few species are evergreen.

In some rural sections the berries, when stewed, are used as a relish for fowl and meat, in place of cranberries, and for making a cool drink. A yellow dye is made from the bark; and the bark, roots, and stem-wood are used as drugs. The European Barberry and some other species are one of the alternate hosts of the wheat-rust (p. 480, *et seq.*). The genus *Mahonia*, like some of the barberries, is evergreen; it has pinnately compound foliage leaves and no thorns. The apparently simple foliage leaves of "barberries" are really compound leaves with only one leaflet, as is shown by the joint in the short leaf-stalk; they are clustered on short spurs in the axils of 1- to 3-pointed spines which are really modified leaves.

LAUREL FAMILY

The Laurel Family (*Lauraceae*), with about 40 genera and 900 species, is largely tropical, but 5 genera (*Persea*, *Nectandra*, *Sassafras*, *Malapoenna*, and *Benzoin*) are common in temperate and sub-tropical America. They are all aromatic trees and

shrubs, with a single carpel like the barberry, but with only one ovule.

The fruit of *Persea gratissima* is known commercially as Avocado, or more commonly as Alligator Pear. The latter name is wholly misleading and should not be used. The species is indigenous to Mexico and Central and South America. Seedlings may attain a height of over 50 feet, but budded trees are not so tall. The fruit varies greatly in shape and size with different varieties, and ripens at all seasons, varying with the variety.

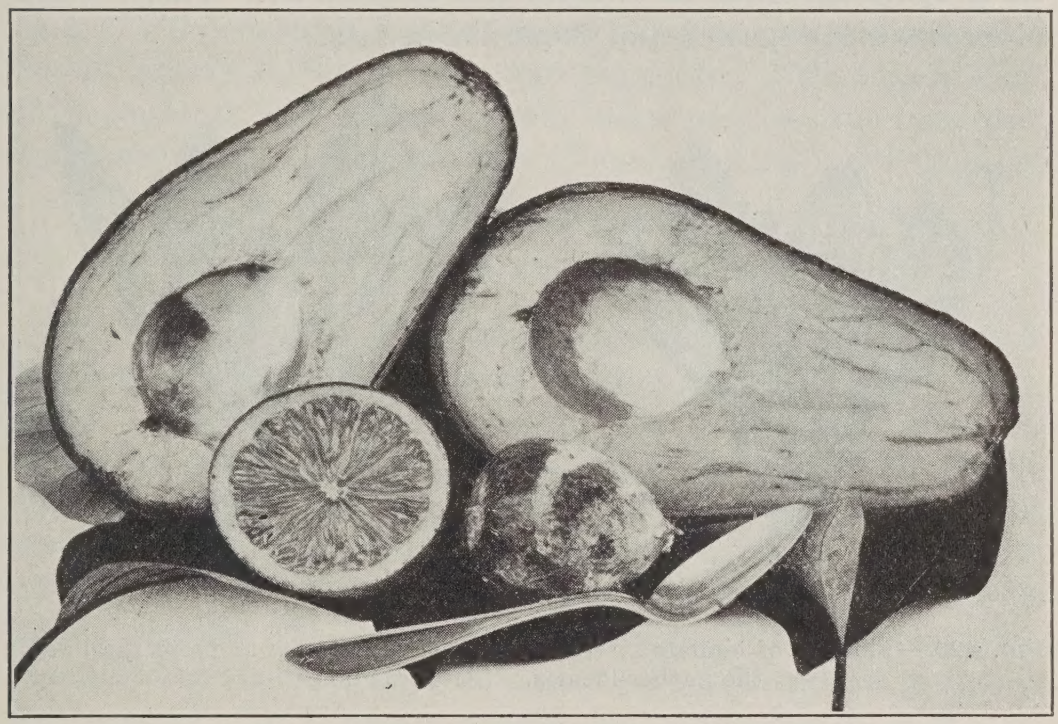


FIG. 419.—A pear-shaped, Mexican avocado, grown in California. Note the large stone-like seed at the right of the lemon. (After F. W. Popenoe. From Mo. Bull. State Comm. of Hort., California, 1912.)

The yellow flesh of the fruit cuts like butter, contains 16–18% of oil, and encloses one large seed (Fig. 419). The name Avocado is corrupted through the Spanish (*ahuacate*) from the Aztec (*ahucatl*).

Persea carolinensis, a tree 60 feet or more high, is the Sweet Bay or Laurel of the southern United States. It is known also as Florida Mahogany, and Red Bog.

Sassafras variifolium, a deciduous tree 12–90 feet or more in height, may be easily identified by the varying shape of its leaves, which resemble either left- or right-handed mittens, or double

mittens. From this character was derived the specific name, *variifolium*. A synonym (*Sassafras officinale*) refers to the pharmaceutical use of the root-bark, pith, leaves, and green bark of the twigs. The only other species, *S. tzumu*, recently discovered in China, is a larger tree with larger leaves than our species.

The Spicebush (*Benzoin aestivale*) is a shrub 3–9 feet high with an aromatic, spicy bark, found in damp woods and along streams in the eastern United States, flowering in the spring and ripening its drupaceous fruits in August and September. There is one other American species, and about five in Asia.

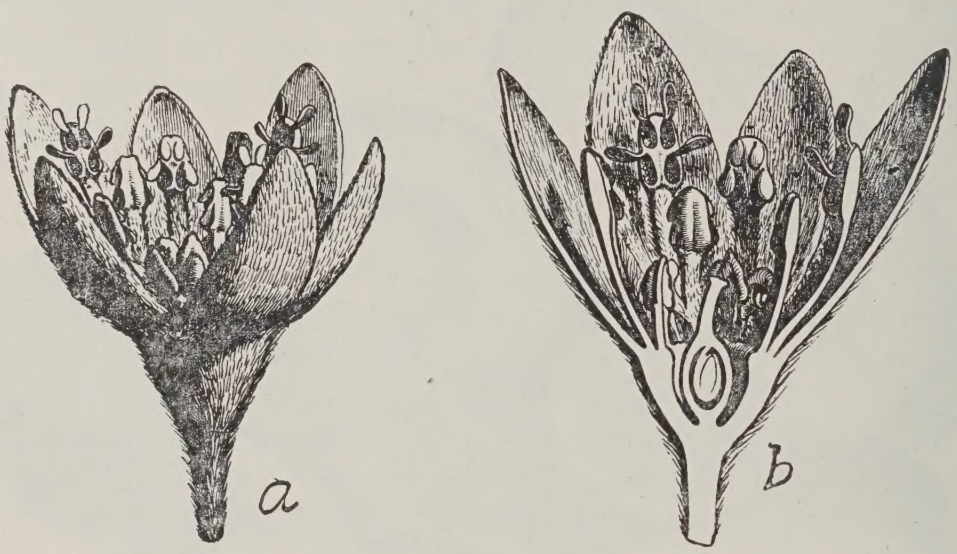


FIG. 420.—Flowers of cinnamon (*Cinnamomum zeylanicum*). Note the lids of the anther-locules. (After Baillon.)

Other genera are *Laurus*, with two species, *L. nobilis* (the Bay Tree of the florists, capable of being clipped into almost any desired shape), and *L. canariensis;* and *Cinnamomum*, tropical and sub-tropical evergreen shrubs and trees, with aromatic bark, leaves, and wood. *C. Camphora* Nees & Eber. (= *Camphora officinarum* Nees), a medium-sized evergreen tree, is planted along roads in southern California. It is native in Japan, China, and Formosa, and is largely planted in India. This species is the most important natural source of camphor,[1] which

[1] Watt states that probably the camphor first known to the world was obtained from *Dryobalanops aromatica* of the Dipterocarpaceae, indigenous in Borneo and Sumatra. Camphor is also obtained from thyme, tobacco, and other plants, but not extensively.

is extracted from the wood, and exported chiefly from Japan and to a less extent from China. The virtual monopoly of this product by Japan led to the perfection of a process for synthesizing artificial camphor in America.

Cinnamomum zeylanicum, larger than the camphor-tree, is native in southern India and Ceylon (Fig. 420). Its cultivation is largely confined to Ceylon. In cultivation the plant is cut back until it grows as a coppiced bush, and the bark of the numerous shoots, when dried, constitutes the cinnamon of commerce. In powdered form true cinnamon is usually adulterated with the bark of *Cinnamomum Cassia* (known in commerce as cassiawood *Cassia lignea*), a Chinese tree, and the source of the Cassia bark of the ancients.[1] "Camphor wood," used for boxes and furniture, is obtained from *C. glanduliferum* (Nepal sassafras), and *C. iners*.

ORDER, Papaverales

POPPY FAMILY

The Poppy Family (*Papaveraceae*) comprises about 25 genera and some 200 species nearly all herbs, with milky juice (*latex*), yellow or saffron in some genera. The 2 (rarely 3 or more) sepals fall off as the flower opens. The stamens are numerous, and the ovules are attached to the wall of the ovary (parietal placentation). The seeds have a minute embryo, imbedded in a fleshy, oily endosperm, and the juice is acrid or narcotic. This family includes the Bloodroot (*Sanguinaria canadensis*), Celandine (*Chelidonium majus*), the Poppies (about 25 species, including the Opium Poppy (*Papaver somniferum*), and a few other genera.

The Opium Poppy was introduced into the United States on ballast, and is becoming established as a wild plant in waste places and near dwellings. In Europe it has been known for some time as a plant that readily escapes from cultivation, but, aside from this, it is not known to exist in a primitive wild state. There is evidence pointing to its derivation from *Papaver setigerum*, which grows wild on the shores and islands of the Mediterranean. The commercial products of the poppy are the oil from the seeds and the white latex which, when hardened, constitutes *opium*. The chief narcotic substance in opium is the alkaloid, *morphine*.

[1] The modern Cassia bark is obtained from *C. zeylanicum*, and *C. Tamala*.

This genus comprises some of the very oldest of cultivated plants; it was cultivated by the Swiss lake-dwellers of the stone-age, and by the ancient Greeks, being mentioned by Homer, and later by Theophrastus. The Chinese invented the custom of smoking opium, and as a habit-forming, narcotic drug it has probably been the cause of more human misery than any other plant product, with the possible exception of alcoholic beverages.

The Bleeding Heart (*Dicentra spectabilis*), more common than now in the gardens of a generation ago, is closely related to the wild *Dutchman's Breeches*. By some botanists this genus, and also the Fumitory (*Fumaria officinalis*) and several other genera, are separated as a family—the *Fumariaceae*.

FIG. 421.—Black mustard (*Brassica nigra*).

Related to the poppies are the Capers (*Capparidaceae*) and the Mignonette (*Resedaceae*) of the florists. The "capers" used in cooking are the flower buds of *Capparis spinosa*.

MUSTARD FAMILY

Practically all plants of the *Mustard Family* (*Cruciferae*) have a sharp, or pungent, watery juice, and the four clawed petals form a distinct Maltese cross, whence the name, Cruciferae (Fig. 421). The four sepals, in two whorls, are deciduous. There are six stamens, four with long filaments, and two, inserted lower down, with short filaments. Such an arrangement of stamens is called *tetradynamous*. The ovary is really *unilocular*, but usually a thin partition grows out from the *placentas*, forming two "cells" or locules. When the ovary is ripe the wall splits along the line of the marginal placentas, the resulting *valves* being either much longer than wide (forming a *silique*), or short (forming a *silicle*). In some genera the fruit is indehiscent. The flowers are sometimes arranged in corymbs, but oftener in terminal racemes. The seeds of several species of *Brassica* yield a commercial oil (Colza- or Rapeoil).

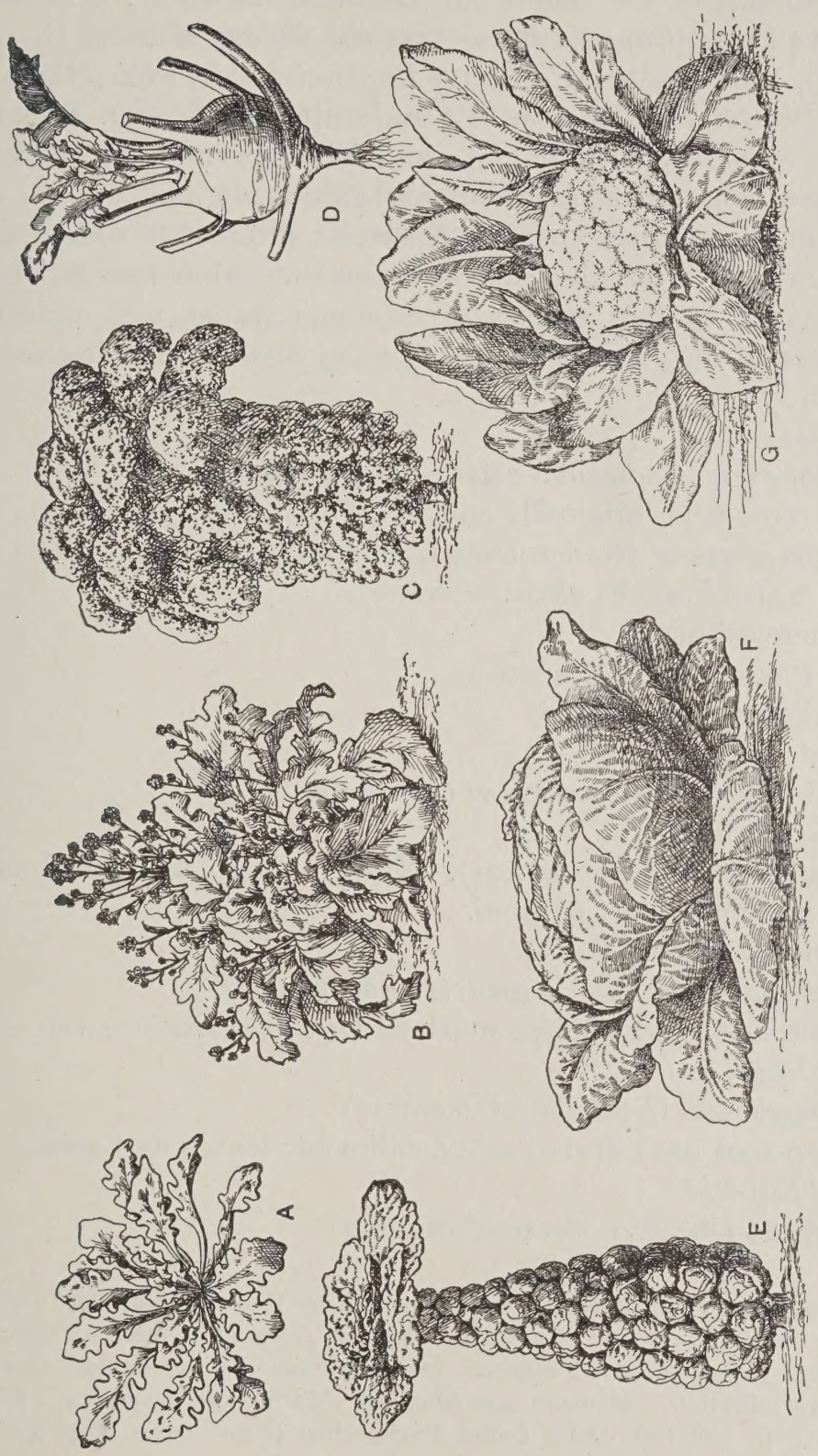


FIG. 422.—Horticultural varieties of the wild cabbage. *A*, wild cliff-cabbage, hypothetical ancestor of the numerous modern horticultural forms; *B*, broccoli (leaves and flowers both used); *C*, kale; *D*, kohlrabi; *E*, brussels sprouts (lateral buds used); *F*, common cabbage (a highly developed terminal bud); *G*, cauliflower (flower-buds used). (Redrawn from various sources.)

Some species of the family are troublesome weeds, such as Shepherd's Purse (*Capsella Bursa-pastoris*), Hedge Mustard (*Sisymbrium*), Wild Radish (*Raphanus Raphanistrum*); while others, such as Stocks (*Mathiola sp.*), Candytuft (*Iberis sp.*), Sweet Alyssum (*Alyssum maritimum*), and Wallflower (*Cheiranthus Cheiri*), are highly prized as ornamental garden plants.

The family comprises about 1500 species, grouped in some 185 genera, and widely distributed over the earth. Numerous genera in the family contain species of economic value, and almost every organ of the plant is used in one way or another, as follows (Fig. 422):

Leaves used

Water-cress (*Radicula Nasturtium-aquaticum*)
(now wild; originally cultivated)
Pepper-grass or Garden cress (*Lepidium sativum*)
Kale (*Brassica oleracea viridis*)
Chinese cabbages
Pak-choi (*B. chinensis*)
Pe-tsai (*B. Pe-tsai*)

Stem used

Kohl-rabi (*Brassica oleracea caulo-rapa*)

Root-and-stem used

Radish (*Raphanus*[1] *sativus*). The "radish" is formed of tap-root and lower part of stem.
Turnip (*Brassica Rapa*)
Rutabaga (*Brassica campestris napo-brassica*)
Tuberous-rooted Chinese mustard (*Brassica napiformis*)

Root and leaves

Horse-radish (*Radicula Armoracia*)
Tap-root used grated as a condiment; leaves as "greens"

Terminal leaf-bud

Cabbage (*Brassica oleracea*[2] *capitata*)

[1] The common English name, *rádish*, refers to the fact that the root (*radis*) is used; the generic name, *Raphanus*, is from the Greek, ῥᾳ (*rhai*, rapidly) and φαίνω, *phaino*, I appear), meaning "quickly appearing," from its rapid germination. Munson and Shepard (Maine Agr. Exp. Sta. 14th Ann. Rept., p. 158–160, 1898) found that radish plants from large seed grow larger and mature earlier than those from small seed.

[2] *Oleracea* (Latin, *holeracea*) = vegetable; of the garden.

Lateral (axillary) leaf-buds

Brussels sprouts (*Brassica oleracea gemmifera*)

Flower buds

Cauliflower and Broccoli (*Brassica oleracea botrytis*)

Seeds

Black mustard (*Brassica nigra*)

White mustard (*Brassica alba*)[1]

Rape (*Brassica Napus*)

[1] *Brassica alba* was called by Linnaeus *Sinapis alba.* Young plants of both black and white mustard are also used as "greens" and in salads.

CHAPTER XXIX

POLYPETALOUS DICOTYLEDONS (CONTINUED)

ORDER, Rosales

The Rosales constitute a very large order, comprising many herbs, shrubs, and trees of great economic importance, from the standpoint of both agriculture and horticulture. The sepals are

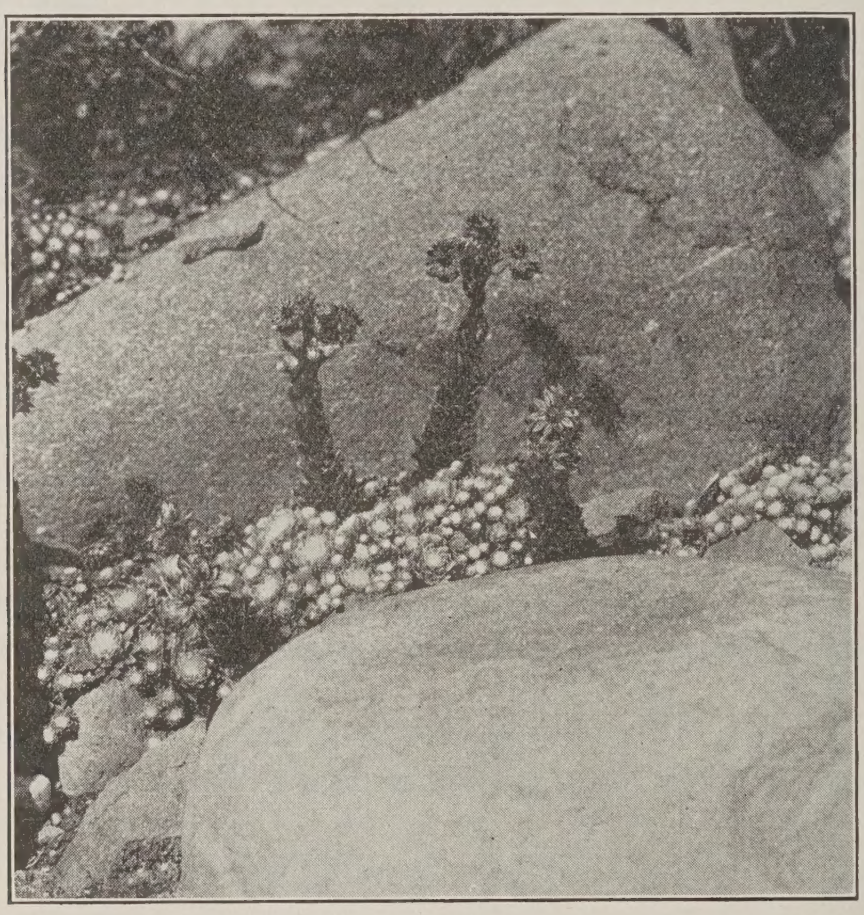


FIG. 423.—Spiderweb Houseleek (*Sempervivum arachnoideum*) in flower. The tips of the leaves are connected with fine white plant-hairs that form a web over each rosette.

more or less united at the base with a receptacle which is either concave (*e.g.*, rose), or convex (*e.g.*, strawberry). The stamens usually numerous) are attached to the calyx.

ORPINE FAMILY

The Orpine family (*Crassulaceae*) contains about 15 genera and some 500 species. The genus *Sedum* has about 150 species, some of which (*e.g. Sedum spectabile*) are highly decorative, and some are much prized rock-garden plants. The houseleeks (*Sempervivum*) comprise the "hen-and-chickens," introduced from Europe, and often escaping from cultivation. *Sempervivum arachnoideum* and other species are valued as rock garden plants (Fig. 423). The leaves of both *Sedum* and *Sempervivum* are modified for the storage of water, and they are consequently very resistant to drought—whence the name, *Sempervivum*, meaning living forever.

FIG. 424.—*Saxifraga sarmentosa* (Mother of Thousands; Strawberry Geranium), showing young plantlets that have formed at the tips of the numerous thread-like stolons.

SAXIFRAGE FAMILY

The Saxifrage Family (*Saxifragaceae*) comprises shrubs and herbs. The leaves are usually without stipules and the seeds have abundant fleshy albumen, in these two respects differing from the rose family. In this family are the various species and varieties of *Saxifraga* and *Heuchera*, beautiful plants specially suited to rock gardens (Fig. 424). The Miterworts (*Mitella*) and the False Miterwort or Foamflower (*Tiarella*), wild flowers in various parts of the United States, also belong here. These genera also illustrate the very interesting and significant fact in the geographical distribution of plants, referred to on page 572, namely, that the plants of eastern Asia and Japan are, as a rule, more nearly related to those of eastern North America than to those of the west coast and mountains. *Tiarella*, for example is native in eastern North America (from Nova Scotia to Minnesota and Indiana, following the mountains as far south as Geor-

gia), and in Japan and the Himalayas. In the same family are the Golden Saxifrages (*Chrysosplenium*), the Grass-of-Parnassus (*Parnassia*), and the so-called Virginia Willow (*Itea virginica*), not a willow, though *Itea* is the Greek word for willow.

The Saxifrage Family is a large one, comprising as many as 600 species grouped in about 70 genera. The genus *Saxfraga* contains approximately 150 species in general cultivation, and most of these propagate by offshoots and stolons (Fig. 424).

The *Hydrangeas* and *Deutzias* are among our most beautiful flowering shrubs. The genus *Philadelphus* contains the cultivated "mock orange;" this shrub, and also other species of the genus, are known by the common name, Syringa, which, as pointed out on page 558, is also the Latin name for the lilac. By some authors the woody genera of the Saxifragaceae are classed in a separate family—the *Hydrangeaceae.*

GOOSEBERRY FAMILY

The currants and gooseberries are classed by some in the Saxifrage Family; by others they are considered as constituting a separate family, the Gooseberry Family (*Grossulariaceae*). By some botanists, also, currants and gooseberries are both considered as belonging to the genus *Ribes*, while others group them in two genera—*Ribes* (the currants), with racemes many-flowered and the stem mostly without spines or prickles; and *Grossularia* (the gooseberries), with 1–4 flowered racemes, and the stems armed. About 60 species of *Ribes* have been described from the north temperate zone of both hemispheres, from the Andes of South America, and from South Africa; of these, about one half belong to the section *Ribes*, and one half to the section (or genus) *Grossularia.* Since certain gooseberries and currants provide the alternate host for the destructive fungus causing the white pine blister rust, they have recently assumed an economic importance much greater than they formerly possessed merely as fruit-bearing shrubs.[1] The northern red currant, *Ribes rubrum* (Fig. 425), grows wild throughout the north temperate zone, and the cultivated plant hardly differs from the wild form. It has

[1] See, in this connection, pp. 528–529.

been cultivated since the Middle Ages, but does not appear to have been known to the ancient Greeks and Romans. Another red currant is *Ribes vulgare*. The European black currant (*R. nigrum*) is native to the old world north temperate zone, ranging from Lapland and Siberia to Italy and Armenia. The American black currant is *R. americana*. The black currants have a disagreeable odor.

The fruit of the wild prickly gooseberry or dogberry, *R. Cynosbati* of the Northern United States, is usually covered

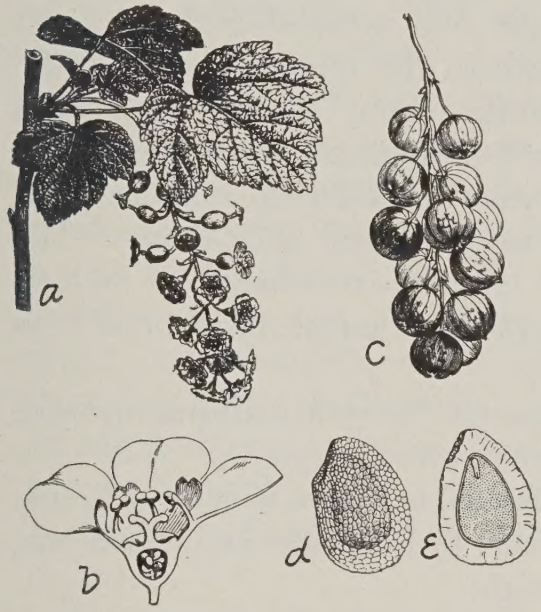


FIG. 425.—Red currant (*Ribes rubrum*). (After Baillon.)

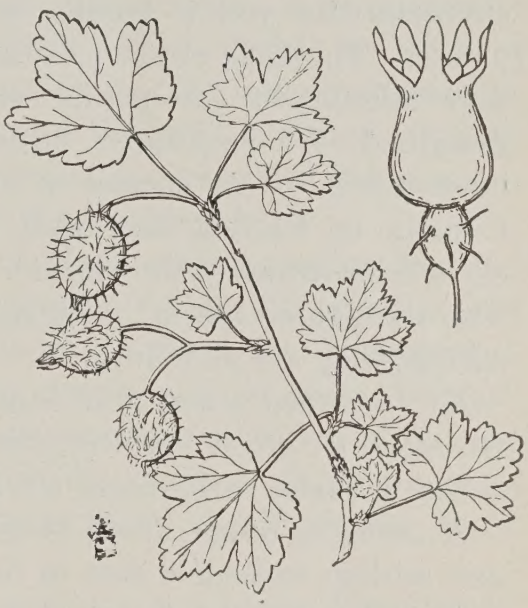


FIG. 426.—Wild prickly gooseberry (*Ribes Cynosbati*). Also called dogberry. (After Britton and Brown.)

with awl-shaped spines (Fig. 426), but these are absent from the English and European forms, which were derived from a smooth-fruited wild ancestor, *R. Grossularia*. The American cultivated forms were derived from *R. hirtellum*, a smooth-fruited species. Cultivated forms have escaped from gardens and become established in numerous places in North America. The gooseberry was originally used by the English as a relish for goose and other fowl, and this is believed to explain the common name, gooseberry. Probably for a similar reason it is called, by the French, "mackerel currant" (*groseille à maquereaux*).

WITCH-HAZEL FAMILY

The Witch-hazel Family (*Hamamelidaceae*) includes only trees and shrubs. The pistil has two united carpels and the ovary is partially inferior. The 15 genera and about 35 species are natives of North America, Asia, and South Africa. In the temperate regions of North America only three genera occur—namely *Hamamelis* (Witch-hazel), *Liquidambar* (Sweetgum), and *Fothergilla.*

The Witch-hazel bears fruits and flowers at the same time, whence the generic name, Hamamelis.[1] The flowers have a characteristic yellow corolla with four strap-shaped (*ligulate*) petals. The four stamens adnate to the sepals are fertile; the four adnate to the petals, sterile. Four species have been described: *H. virginiana* flowers in autumn after the leaves have fallen. This species is native to America, ranging from Canada to Florida and west to Nebraska and Texas. The calyx is brownish yellow inside. It grows to a height of 25 feet. The other three species, with calyx red or purple inside, flower in spring; they are as follows:

H. Japonica, a native of Japan, has two horticultural forms or varieties, *H. arborea* and *H. Zuccariniana.*

The Chinese witch-hazel (*H. mollis*) is native in central China.

H. vernalis ranges from Missouri to Louisiana and Oklahoma, and seldom exceeds 6 feet in height.

The Witch-hazel flower does not open until after the leaves have fallen in autumn. For this reason it has (somewhat facetiously) been called the "earliest spring flower." This genus is the source of the extract of witch-hazel of commerce. The name witch-hazel doubtless refers to the supposed property of a forked branch, when carried horizontally near the ground, of bending down, and thus indicating the presence of underground water in quantity sufficient to justify the digging of a well. The belief was always and inherently absurd, and is no longer held, except by credulous or uninformed persons.

The Sweetgum (*Liquidambar Styraciflua*) becomes a large shade tree, with beautiful autumn foliage, and yields the liquid styrax of the pharmacopaea.

[1] Hamamelis, from the Greek, ἅμα (*hama*), at the same time, and μῆλον (*mēlon*) fruit.

PLANE TREE FAMILY

The Plane Tree Family (*Platanaceae*) contains only one genus, *Platanus*. The "button-ball" or Plane Tree, of the northeastern United States, is *Platanus occidentalis*.

ROSE FAMILY

The family of the Roses (*Rosaceae*) takes its name, of course, from the "queen of flowers," the rose. Its 1200 species, more or less, are grouped in about 65 genera of trees, shrubs, and herbs, of wide distribution. The leaves, alternate as a rule, usually have stipules, sometimes quite large. The carpels are distinct and not adnate to the calyx, or rarely so. The numerous stamens are inserted on the calyx tube, and the fruit is either a follicle (*e.g.*, *Spiraea*), an aggregate of achenes (*e.g.*, rose and strawberry), or an aggregate of drupelets, as in the blackberries.

The fruits (ripened ovaries) of blackberries, raspberries, and dewberries, are not, in reality, berries (Cf. p. 407) but, as just noted, are drupelets which adhere to form an "aggregate" fruit (Fig. 427). Pollination is by insects. These three "berries" belong to the genus *Rubus*, of wide geographical distribution, and a very difficult group, systematically, on account of its great variability. Some authors make as many as 250 species, more or less.

The so-called "strawberry"[1] is also not a berry, botanically, but consists of a fleshy, juicy receptacle, bearing many scattered fruits (achenes) which are commonly called seeds (Fig. 428). The size of the fruit depends upon the number of pistils that are pollinated. This is a distinctly American fruit, the modern cultivated forms having been largely derived from the North American species, *Fragaria virginiana*, and the South American species, *F. chiloensis*. The early American colonists depended at first on the abundant supply of wild berries in the

[1] The name is from the Anglo-Saxon word, *streawberie* or (later) *straeberie*. The Anglo-Saxon verb *streáwian* means to scatter or strew. It is likely that the word refers to the habit of producing runners which spread the plant. It has also been suggested that the name refers to the strewing of straw among the plants to keep the berries off the ground, but the name (in its Anglo-Saxon form) antedates the cultivation of the plant. Concerning the pollination of the strawberry see p. 372, *et seq.*

fields, but after a time they began to cultivate the plant (*F. virginiana*) in gardens. Cultivated varieties have been derived by mutation (seedling sports[1]) from *F. virginiana* and *F. chiloensis*, and by hybridizing between these two. Some forms are the result of crosses between *F. virginiana* and *F. elatior* (the "Haut-

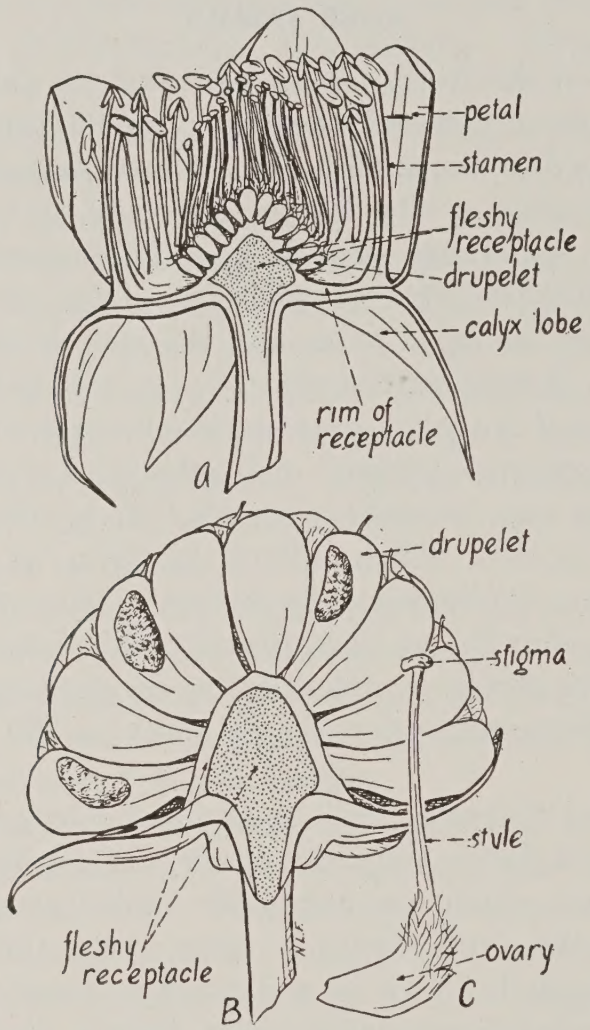


FIG. 427.—American red raspberry (*Rubus strigosus*). A, median longitudina section of the flower, × 4; B, same of fruit, × 4; C, single immature pistil, × 5. (After Robbins.)

bois"). The famous "Hovey," produced by C. M. Hovey in 1834, was the result of a cross, but the labels were lost and the parentage is therefore unknown. The element of size was probably contributed by the Chilean species, and flavor by the Virginian. No garden forms of value have ever come from the

[1] There is said to be no authentic instance on record of bud-sporting in the strawberry.

European wild strawberry (*F. vesca*). Albinos or white fruited forms of this species are not uncommon. The generic name, *Fragaria,* has reference to the fragrant odor of the ripe fruit. Both the Virginian and the Chilean species were introduced into Europe, the former in the early seventeenth and the latter in the early eighteenth century. In the middle of the eighteenth century there appeared in Europe a new horticultural variety—

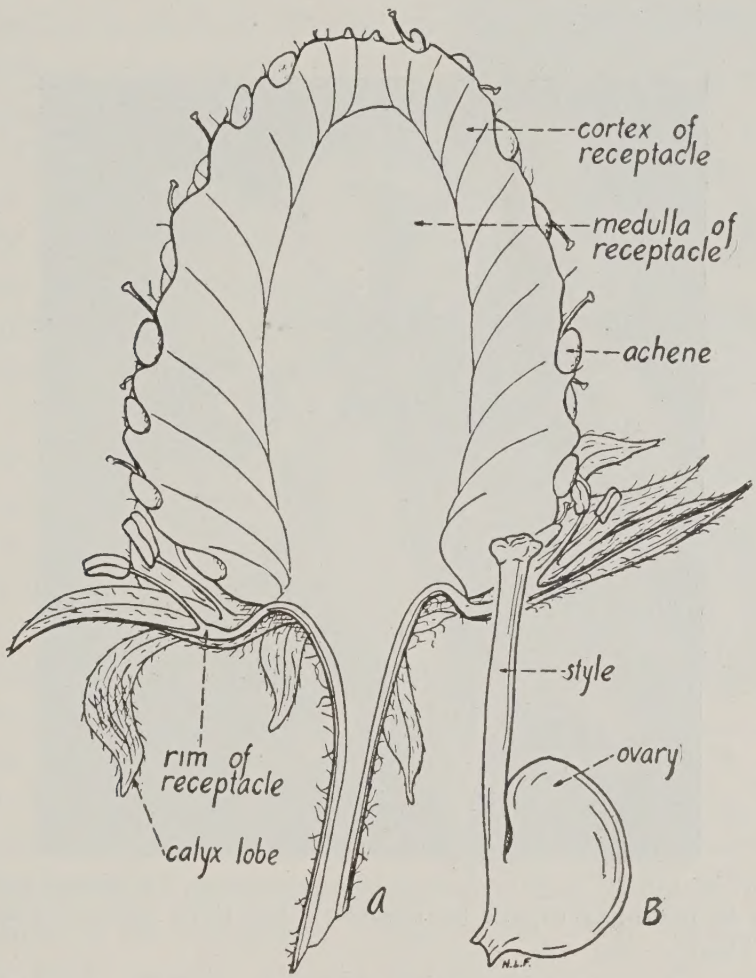


FIG. 428.—Strawberry (*Fragaria chiloensis*). A, "fruit" in median longitudinal section, × 2½; B, single fruit (achene). (After Robbins.)

the "Pine" or "Pineapple." The ancestry of the Pine is not certainly known, but there is considerable evidence that it resulted from a cross between *F. virginiana* and *F. chiloensis.* Whatever may have been its origin, its importance can hardly be exaggerated, for it became the progenitor of many of our most successful garden varieties. "Ever-bearing" varieties have recently been bred from other garden forms.

The genus *Rosa* contains some 12 or 15 wild species in the eastern United States, and 5 or 6 more in the west and south, but the wealth of horticultural varieties is legion. Most of the latter have double flowers, resulting from the fact that petals occur at the points where stamens normally develop (Fig. 429). It is beyond the purpose and scope of an introductory text-book to discuss the various groups and the innumerable horticultural varieties of the rose.

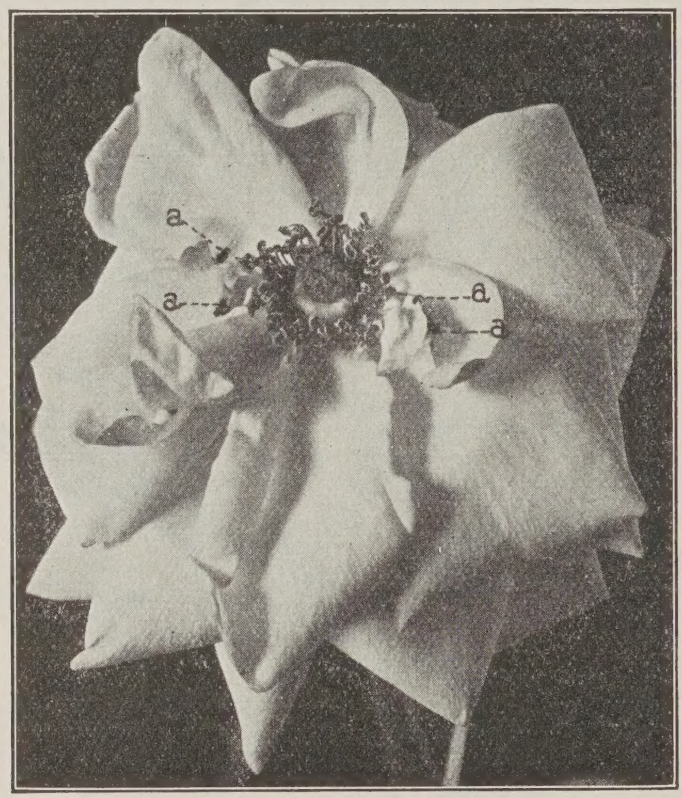


FIG. 429.—Petalody of stamens in a cultivated rose. *a*, indicates the remains of anthers on petal-like organs (*staminodia*) that have replaced stamens. (Cf. Figs. 242, 243.)

APPLE FAMILY

The 20 or more genera that constitute the Apple Family (*Pomaceae*) are considered by some botanists as belonging to the Tribe *Pomeae*, of the family Rosaceae. They are all trees or shrubs, and the *pomaceous* fruit with the united carpels (forming the "core" in the fruit, Fig. 430), the enclosing of the carpels by the adnate calyx tube, Fig. 431, and certain other characters afford a basis for grouping them in a separate family. Here belong the pears and apples and, among trees uncultivated

or cultivated only for their beauty, the Mountainash (*Sorbus*), Chokeberry (*Aronia*), Juneberry (*Amelanchier*), known also as Shadbush or Serviceberry, the Thornapple, Hawthorn or Haw (*Crataegus*), and *Cotoneaster*.

Most of our cultivated apples, except the crabs, appear to have come from the wild apple of southwestern Asia and southeastern Europe. Linnaeus called this wild apple *Pyrus Malus*. There are valid botanical reasons for classifying the pears and apples under two genera. The pears (*Pyrus*) are distinguished from the apples (*Malus*) by usually having stone-cells in the fruit; these are absent from the fruit of the apples. The cavity or depression about the stem of the apple is absent from the pear, the region being convex. The styles of the pear are also separate, those of the apple more or less united at the base. There are also other differences.

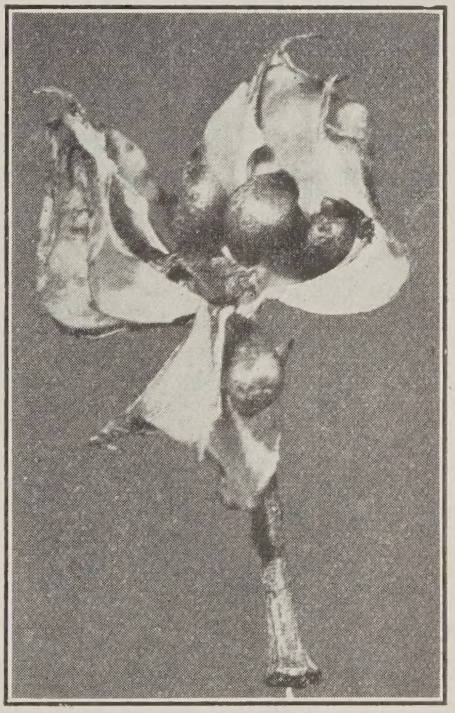


FIG. 430.—Ripened ovary ("core") of an apple. Note the five membranous or papery carpels, and the seeds within, attached to the margins of the carpels (axillary placentation). The edible portion, composed largely of the tissue of the receptacle, has been removed. Photo from nature. *Cf.* Fig. 431.

The apples formerly designated as *Pyrus Malus* L. are now described under two species, *Malus pumila* Miller and *Malus sylvestris* Miller. *M. pumila* is regarded as the probable ancestor of our cultivated large apples, with possibly an admixture in some of them of *M. sylvestris*. The cultivated crab apples appear to have been derived from the wild crab, *M. baccata* Borkhausen (=*P. baccata* L.).

The apple has been cultivated from prehistoric time. Remains of the fruit are found in the Lake Dwellings of Switzerland. The flowering crab (*M. floribunda*) is extensively cultivated for the beauty of its flowers. This tree is not known wild, but is common in cultivation on account of its striking beauty when in flower. It is thought to be a possible hybrid between two other species.

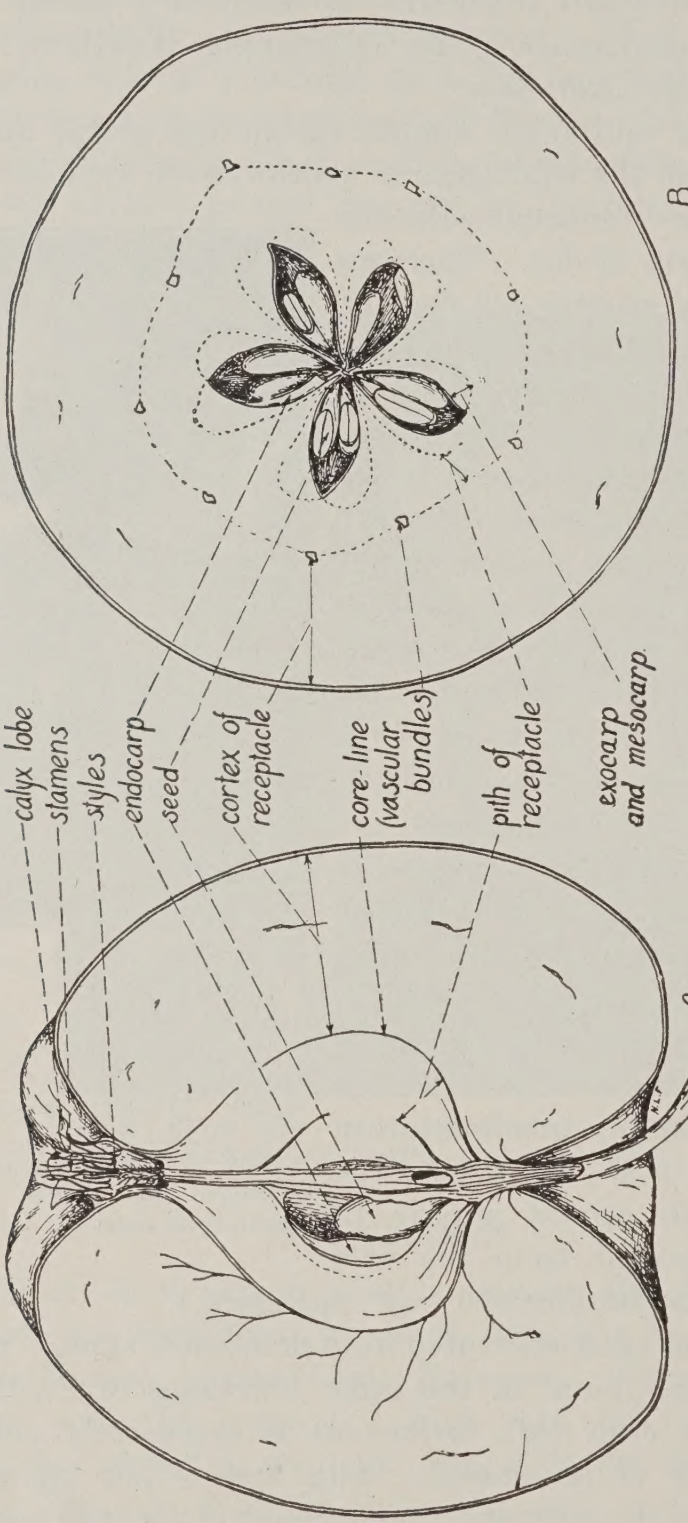


FIG. 431.—Structure of the fruit of the apple. A, median longitudinal section; B, cross-section. (After Robbins.) *Cf.* Fig. 254.

The cultivated pears are varieties of *Pyrus communis* L., native in southern Europe and Asia, of *P. serotina* Rehder, of China, and hybrids between the two (*e.g.*, Kieffer pears). *Pyrus communis* is found wild in the temperate parts of Europe and Western Asia, and has been cultivated at least from the time of Homer (about 1000 B.C.).

Spurs.—In both pears and apples there are two types of shoots—rapidly growing *long shoots*, which bear only leaf-buds, and short shoots or *spurs*, on the tip of which are borne the mixed flower-and-leaf buds, and on which, therefore, the fruit develops. Flower-and-leaf buds are often formed on the end of the longer branches. By orchard men these are called "terminal buds."

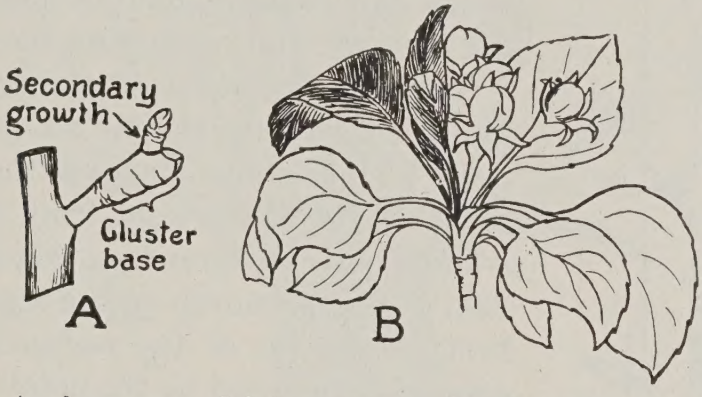


FIG. 432.—Apple spurs and inflorescence. The blossom bud produces two kinds of growth; the cluster-base, upon which the blossoms are borne, and a secondary growth. The latter seems to function largely as does a vegetative spur of like dimensions. (After R. H. Roberts. Univ. Wisconsin Agr. Exp. Sta. Bull. 317.)

Sometimes, and particularly in certain varieties, the flower buds are *lateral.* In addition to flowers and leaves, the flower buds form a new woody growth on which the leaves and flowers are borne (Fig. 432). This is known as the *cluster-base*, and is often found attached to the stem (peduncle) of an apple that has been picked. There is often a lateral secondary growth formed on the cluster base, and which functions like a small vegetative spur.

The spurs are formed early in the season from lateral buds, and bear only foliage leaves the first year. Their growth is usually completed before the end of May. The terminal flower-buds begin to form early, nearly a year before the flowers appear, and their development is complete by early fall. It is not always easy, especially for a novice, to distinguish the leaf-buds from the

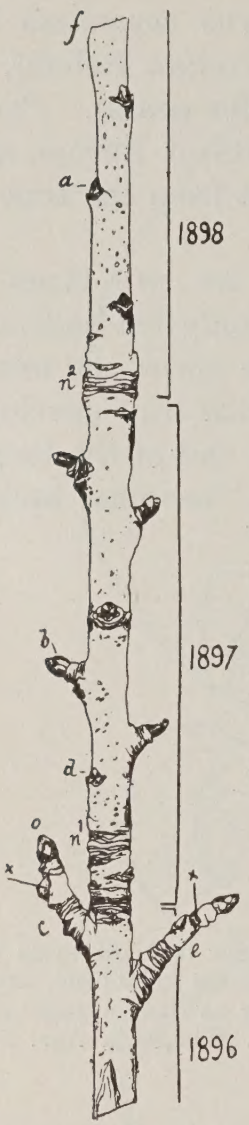


FIG. 433.—Portion of branch of an apple tree, showing two nodes, n^1 and n^2, and portions of three *long shoots* or internodes. The nodes are marked by the scars of the bud scales of the successive terminal buds formed each year. n^2-*f* is *long shoot* of last season, bearing wood-buds (*a*); the long shoots the preceding years have *spur-shoots* which terminate in fruit buds, *b* and *o*; *x*, scars where apples were borne. The smaller size of the scar on spur *e* indicates that the apple fell before it matured. (After Percival.)

flower-buds, but it is highly important to be able to do so, especially in trimming a tree, where care should be taken not to prune away too many of the spurs (Fig. 433).

The pear flower is *epigynous*, *i.e.*, the ovary is *inferior* (Fig. 434). The fleshy part of the pear fruit (or *pome*) is composed chiefly of a portion of the flower-stem (peduncle), and the calyx-tube and receptacle. As the fruit matures, the inner walls of the ovary (*pericarp*) become tough and membranous (or horny), forming the *core*, and containing the seeds.

The interpretation of the fruit of the apple (*Malus*) is similar to that of the pear. The various stages in the development of the flower and fruit have been worked out by Kraus, as shown in Fig. 253.[1] The primordia of the sepals appear first at the tip of the peduncle (the receptacle), followed by the petals, stamens, and carpels in the order named. While these parts are developing the edge of the receptacle develops rapidly, forming a cup. All the floral organs are thus seen to be outgrowths of the receptacle.

Cross-pollination is the rule with apples and is accomplished chiefly by honey bees, and to a lesser extent by other insects.[2]

The studies of Kraus have shown that the flesh of the apple is not, as was formerly generally supposed, the thickened calyx-

[1] Kraus, E. J. The pollination of the pomaceous fruits. I. Gross morphology of the apple. Oregon Agr. Exp. Sta. Res. Bull. I, pt. 1: 1–12. 1913.

[2] Additional facts concerning self-fertility and self-sterility are given in Chapter XVII.

tube, but is produced by the thickening of the receptacle and carpels, which are intimately united.

Alternate Bearing.—Some apple trees bear each year but other trees, and especially certain varieties, bear only in alternate years. The phenomenon of alternate bearing is not perfectly understood, but it appears to be related to nutrition. There is

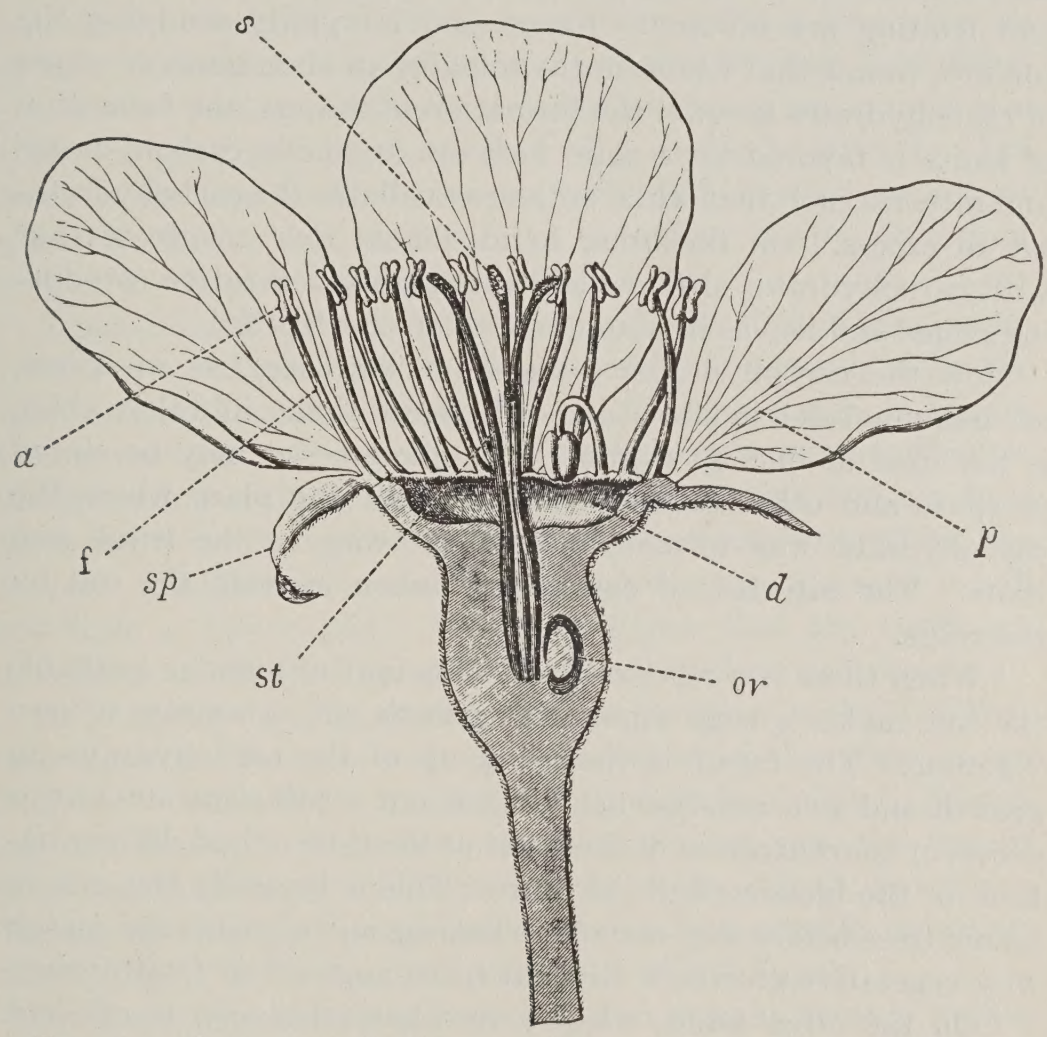


FIG. 434.—Flower of a Bartlett pear in sectional elevation. *st*, style; *sp*, sepal; *f*, filament; *a*, anther; *s*, stigma; *p*, petal; *d*, disk; *ov*, ovule. (After M. B. Waite. U. S. Dept. Agr. Div. Veg. Path. Bull. 5.)

evidence that every second year the tree is engaged chiefly in elaborating plant food which is stored in the trunk, and that in alternate years this stored food is drawn upon by the fruit buds, and the tree bears a good crop. Studies by Roberts[1] led

[1] Roberts, R. H. Off-year apple bearing. Univ. Wisconsin Agr. Exp. Sta. Bull. 317. July, 1920.

to the conclusion that overbearing one year is not the cause of the "off-years," as is commonly surmised, nor can the off-year be charged to the weather.

It is known that a relatively abundant supply of nitrates favors the vegetative activity of a plant, but that, when the supply of carbohydrates is relatively greater than that of nitrates, flowering and fruiting are favored. Kraus and Kraybill,[1] studying the tomato, found that while (in the tomato) an abundance or excess of carbohydrates favored the formation of flowers, the formation of fruits is favored by a ratio between available carbohydrates and nitrates such that while both are available the carbohydrates are in excess. On the other hand, plants rich in nitrates but with carbohydrates also available are highly vegetative (producing stems and leaves in abundance), but not fruitful.

Now the carbohydrates (sugars and starches), as we know, are manufactured in leaves and other green tissue, and that which is not used at once is stored. In apple trees it may be stored in spurs and other branches located near the place where the carbohydrate was formed, or farther away, in the trunk and roots. The nitrates, of course, are taken in from the soil by the roots.

"When there is a relatively large amount of nitrates available the tree makes a large amount of growth, or, as we say, is very vigorous. The result is the using up of the carbohydrates in growth and as a consequence there is not a sufficient amount or excess or concentration of these left at the time of bud differentiation for the blossom buds to form. This is typically the case in young trees before they come into bearing and explains the reason why vegetative growth is thought to be opposed to fruitfulness.

"On the other hand, when a tree has relatively insufficient nitrate and makes little growth, little blossom bud formation occurs. This may be illustrated by the over-blossoming tree when it forms no blossom buds for fruiting the next year. Again, if the tree has a relatively balanced food supply and makes a moderate growth, blossom buds are formed in abundance. This condition prevails in the off-year tree which forms blossom

[1] Kraus, E. J., and H. R. Kraybill. Vegetation and reproduction with special reference to the tomato. Oregon Agr. College Exp. Sta. Station Bull. 149. Jan., 1918.

buds preparatory to producing its usual overload of blossoms the next season.

"This same conception of fruitfulness seems to have equal application as an explanation for the fact of the heavy blossoming of root-pruned, girdled, or injured trees or parts of trees: the transfer of carbohydrates which takes place in the inner bark, outside the wood, is interrupted and the resulting concentration of these substances above the injury causes blossom bud differentiation. The dying tree is practically always an injured tree either in the trunk or roots, that is, it is partly girdled. The result is the formation of blossom buds. This tree does not set about to form them in order 'to reproduce itself;' it cannot help it."[1] (See, however, pages 73 and 75.)

Again, not all spurs bear flowers, and not all flowering spurs bear fruits. Spurs vary in length and, in general, only the medium length spurs, averaging about 12 mm. (½ inch) in length, bear flowers and set fruits, for they have a larger number of leaves in proportion to their bulk than do longer spurs, and are thus more richly nourished with carbohydrates manufactured by the leaves. If all leaves are artificially removed from a spur it will not form a flower bud. This is evidence that the spurs are nourished chiefly by the food elaborated by their own leaves.

In biennially bearing apples such, for example, as the Wealthy, spur growth follows a biennial cycle, most of the spurs on an "off-year" being of the average length most favorable to flowering and fruiting. Therefore, on the following year the tree is loaded with blossoms and bears a heavy crop of fruit, but forms during this fruiting year no spurs or secondary growths favorable for fruiting. Thus the third year is an off-year again.

From studies of biennial bearing and annual bearing apples of the York variety, Hooker found that biennial trees were deficient in carbohydrate the year of bearing, and were deficient in nitrogen in the "off" year. Trees that overproduced biennially were made to bear annual crops by applications of nitrate of soda about the middle of September for four consecutive years. This nitrogen, absorbed by the roots, was stored in the tree over winter and, the following season, "tended to promote carbohydrate

[1] Quoted from Roberts, *l.c.* I have drawn freely on the authors cited in this treatment of alternate bearing.

accumulation in the non-bearing spurs and thus favored blossom-bud formation."[1]

Annual Bearing.—Roberts points out five principal ways in which annual bearing may result:

1. Formation of blossom buds on some secondary growths. This gives successive blossoming of some spurs.
2. Formation of some terminal and lateral blossom buds.
3. Greater growth of the spurs with less than the usual excessive numbers of spurs blossoming and thus some spurs alternating in bearing.
4. "Normal" fruit-spur formation on second year wood.
5. Sufficient growth of non-blossoming spurs on fruiting trees so that they form blossom buds that open the following spring. Thus, bearing on alternating spurs gives regular bearing of the tree as a whole. The last two conditions are most important.

Ripening.—Green apples contain large quantities of starch and of malic acid. In ripening the starch is converted into cane sugar (sucrose) and a mixture of glucose and fructose, called "invert" sugar. This is brought about by the action of a starch-splitting enzyme in the cells. At the same time the malic acid disappears and the fruit thus loses its characteristic sourness. The mellowing of the flesh results from the softening of the *middle lamella* of its cells.[2] In some varieties this occurs in such a way and to such an extent as to make the apple "mealy."

Cider and Vinegar.—The freshly expressed juice of apples is "sweet" cider. When allowed to stand, its alcoholic content gradually increases as a result of *alcoholic fermentation*, produced by the presence of yeast; the result is "hard" cider. This process is followed by *acetic acid fermentation* (caused by a species of bacterium) which converts the hard cider into vinegar. This organism often forms mat-like colonies known as "*mother of vinegar.*" (Cf. p. 544.)

The Quince (*Cydonia oblonga*) also belongs to the Pomaceae, but is not extensively cultivated in America. The Flowering Quince (*Chaenomeles* (or *Cydonia*) *japonica*) is more extensively

[1] Hooker, Henry D. Annual and biennial bearing in York apples. Univ. of Missouri, Agr. Sta. Res. Bull. 75, Columbia, Mo., April, 1925.

[2] The middle lamella is the middle layer of the thickened wall between two adjacent cells.

grown for the beauty of its flowers. The genus *Chaenomeles* is distinguished from *Cydonia* by its crenate or serrate leaf margins, those of *Cydonia* being entire. The styles of Cydonia are free, those of *Chaenomeles* connate.

PLUM FAMILY

The plants of the Plum Family (*Drupaceae*) have a superior ovary composed of one carpel. It is named from its characteristic "stone" fruit, or *drupe*, which results from the hardening of the inner tissue of the carpel, the *endocarp*. This is surrounded by fleshy *mesocarp*, covered with skin or *exocarp*. Examples are plums, cherries, apricots, peaches, and almonds. In Almonds (*Prunus Amygdalus* Stokes = *Amygdalus communis* L.) the "flesh" is thin and dry, and the seed itself is used as food. Seeds of almond and peach, and also the leaves of cherries, sometimes contain a poisonous glucoside, *amygdalin*, which may become converted into the deadly poison, prussic acid, by the action of an enzyme.

The flowers are either solitary, as in the apricot, in corymbs as in the Mahaleb or perfumed cherry (*Prunus Mahaleb*), in umbel-like clusters, as in the Bird Cherry (*Prunus pennsylvanica*) and Beach Plum (*Prunus maritima*), or in racemes as in the Choke Cherry (*Prunus virginiana*). It is not essential here to distinguish the numerous horticultural varieties of plums, cherries, and peaches.

PEA FAMILY

In the last family or families of the Rose order the flower has a single carpel which ripens into a pod or legume. By some botanists the species of this group are classed in one family, the *Leguminosae* with three sub-families (*Mimosoideae*, *Caesalpinoideae*, and *Papilionoideae*); by other botanists they are classed in separate families, including *Mimosaceae*, *Caesalpinaceae*, and *Papilionaceae*.

The main characteristics of the flower have been noted in Chapters I and XVII. Its structure varies greatly in the different groups, but the fruit is, in most cases, a legume, of many seeds, though it may, in some genera, be a dry indehiscent fruit, or even a drupe or a berry. The Mimosa Family includes the inter-

esting "sensitive plant" and the beautiful cultivated acacias of our greenhouses and florists. The Caesalpinaceae comprise the Wild Senna (*Cassia marilandica*) and its relatives, the Honey Locust (*Gleditsia triacanthos*), and the Kentucky Coffee-tree (*Gymnocladus dioica*). The *Papilionaceae* (Pea Family), with some 320 genera and 5000 species, contains some of the most important economic plants of the world, including the Sweet Pea (*Lathyrus odoratus*), Garden Pea (varieties of *Pisum sativum*), the common Kidney Bean (*Phaseolus vulgaris*), Broad Bean (*Vicia Faba*), Lentil (*Ervum Lens*), Soybean (*Glycine Soja*) of China and Japan, and Alfalfa.

Some of the species, especially of the old world, are officinal; for example, *Myroxylon toluiferum* H. B. & K. (= *Toluifera Balsamum* L.) which yields toluol (and also vanillin) from the balsam canals of its cortex, and *Myroxylon Pereirae*, of San Salvador, from which Peruvian balsam is obtained.

Here also belong the Locust tree (*Robinia Pseudacacia*), the *Wistaria*, the *Indigofera tinctoria* (an East Indian plant that yields the dye, *indigo*, now produced synthetically from coal-tar), and *Glycyrrhiza glabra* (which supplies *liquorice root*, and other forms of commercial liquorice). The Locust (*false acacia*) is a native of North America, and was named *Robinia* by Linnaeus in honor of Jean Robin (1550–1629), herbalist to King Henry IV of France, and his son Vespasian (1579–1662), who were the first to cultivate the tree in Europe, where it has now become naturalized.

The genus *Wistaria* was named by Thomas Nuttall (an early student of American plants) after Professor Caspar Wistar,[1] a noted anatomist of Philadelphia. Two species of *Wisteria* are native in Eastern North America, viz: *W. frutescens*, found in low, moist grounds from Virginia to Florida; and *W. macrostachys*, growing in or near swamps from Indiana to Kansas and Louisiana. The Chinese Wisteria (*W. sinensis*) is more showy than the American species, and is more commonly cultivated than *W. frutescens*.

[1] One branch of the family spelled the name Wister, and the genus was spelled *Wisteria* by Nuttall. The correct spelling would have been *Wistaria*.

Alfalfa or Lucerne (*Medicago sativa* L.), derives its common name, alfalfa, from the Arabic, *alfaçfaçah*, which means "the best fodder," while the name lucerne is from the Provençal word *luserno*. In England it is commonly called Purple Medick. The generic name *Medicago* is derived from the country Media, east of Mesopotamia, though the latter country is commonly believed to be the original home of alfalfa. It has been cultivated there since prehistoric times. From thence it was carried in succession, to Arabia, Egypt and Persia, Greece, Italy, France, Germany, and England (1573). It is said to have been taken to Greece by the Persians under Xerxes in 490 B.C. It was introduced into South America by the Spaniards during the early 16th century, reaching New England during the colonial period.

Alfalfa is an upright perennial with a hollow branching stem growing one to three feet high. The leaves bear three leaflets, and the small flowers (purple, blue, or yellow) are borne in thick short racemes. The downy leguminous pods are coiled two or three times spirally. The long tap-root may extend as much as 15 feet into the soil, and this character makes the plant remarkably resistant to drought. Its importance as a forage plant in the United States, especially in the west, has greatly increased during the past few decades. The name alfalfa includes several species of *Medicago*.

It was formerly thought that the vitality of alfalfa seed was so low that seed over one year old was scarcely worth sowing. Recent studies by Headden, however, demonstrate "that good, sound, clean alfalfa seed, kept under fair, not ideal, conditions will retain its vitality for 23½ years without any perceptible abatement. Further that good commercial seed, preserved under rather disadvantageous conditions retains a fair degree of vitality, 46 per cent., for 27½ years. Further, that very inferior seed, third quality screenings, kept under rather indifferent conditions still contained 16.5% of viable seeds when 22½ years old."[1]

Macmillan has also recorded observations showing that pieces of alfalfa roots left in the soil for more than one year are still capable of producing plants from adventitious buds. "Such

[1] Headden, Wm. P. The vitality of alfalfa seed as effected by age. Proc. Colorado Sci. Soc. **11**: 239–249. June, 1919. (*Cf.* pp. 153; 108–110.)

vitality," as Macmillan says, "in the world's greatest forage crop is certainly a valuable asset."[1]

The Peanut (*Arachis hypogaea*) is botanically interesting on account of peculiarities in the structure of its flower, and also on account of its habit of maturing its fruit underground. The long-petioled leaves are abruptly pinnate, with four leaflets and no terminal tendril such as occurs in the garden pea (Fig. 435).

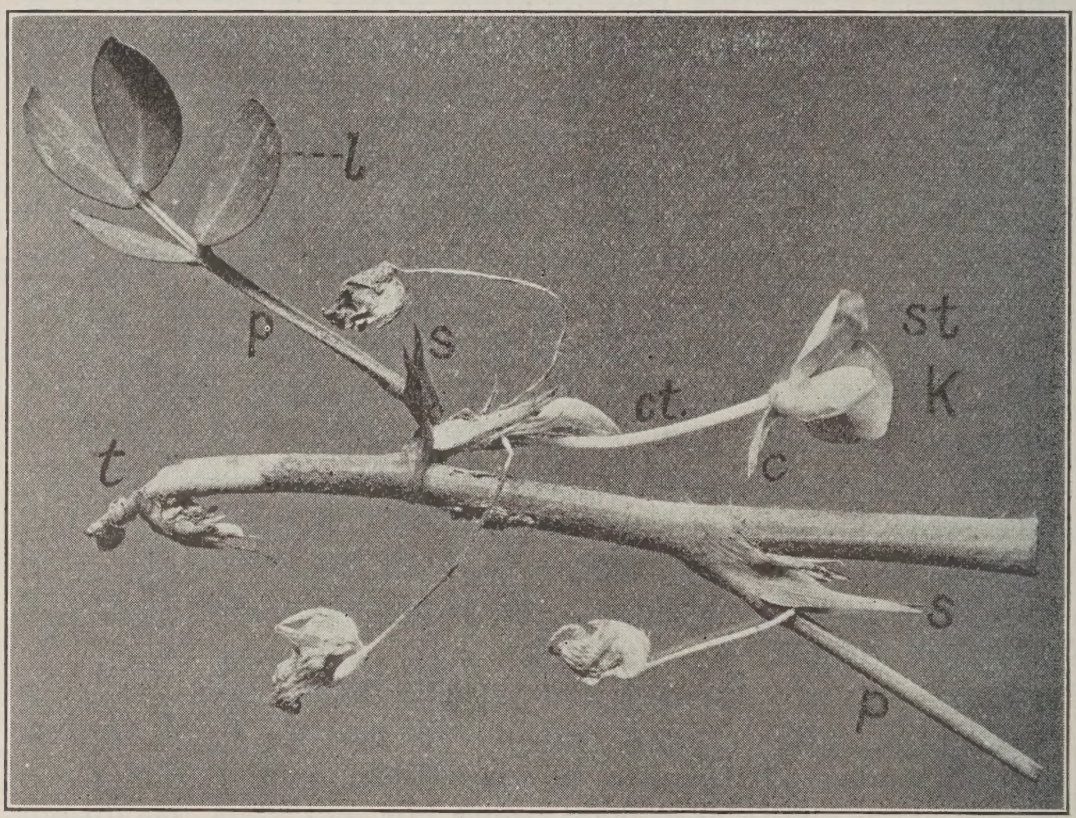


FIG. 435.—Terminal portion of peanut stem (*Arachis hypogaea*). *l*, one of the four leaflets of the compound leaf; *p*, petiole; *s*, stipules; *t*, tip of the stem; *ct*, calyx tube, through which extends the long style; *c*, the anterior, free sepal; *st*, standard of the corolla; *k*, keel.

The elongate stipules are adnate to the leaf-stalk. The bright yellow flowers, borne 5–7 together in the axils of the lower leaves, are of the papilionaceous type, but what appears superficially as a peduncle is a long straight calyx-tube. Of the sepals, the anterior one is free, the four other parts united. The petals, borne on the throat of the calyx-tube, are very unequal, the standard thick and gibbous at the back, and the carina or keel

[1] Macmillan, H. G. The vitality of alfalfa roots. Proc. Colorado Sci. Soc. **11**: 251–252. July, 1919.

attenuated and beaked. The nine stamens are united in a tube, with the anthers unequal. The ovary, enclosed by the lower end of the calyx-tube, is attached to the receptacle by a very short stalk, called the *stipe* or *gynophore*. After pollination the perianth drops off and the stipe increases greatly in length, bending down geotropically, and forcing the small, pointed ovary into the soil. Here the ovary matures, assuming the well-known characters of the commercial peanut (Figs. 255 and 436),

FIG. 436.—Portion of a peanut field, showing one hill with the "nuts" exposed. (After Beattie, U. S. Dept. Agr. Farm. Bull. No. 431.)

and enclosing from two to three (rarely more) seeds, each surrounded by a thin friable testa, brown and loose in the roasted nut. The two "halves" of the seed are the cotyledons, rich in starch and oil. The embryo is relatively large and straight (not curved as, for example, in the bean).

In addition to the use of the nuts for food, confections, peanut butter, and peanut oil, the shoots (usually with a few pods adhering) are used as fodder for hogs and cattle, and also as

green manure. Peanuts may be grown as a crop throughout the southern portion of the United States, from coast to coast. They are known in various sections by different names, such as ground-nut, goober, goober-pea, and pindar. The generic name (*Arachis*) means "having no rachis" or stem (that is, main stem), and the specific name, *hypogaea*, means "under the ground," referring to the habit of development of the fruit.

There are two general types as to the manner of bearing the "peanuts," namely "running" and "bunch." In the former the vines have spreading branches that grow flat on the ground and bear pods at the nodes almost throughout their length. In the latter type the branches grow erect, and the pods are produced closer up around the tap-root.

The peanut has never been found in a wild state, but it is generally regarded as a native of Brazil. It was introduced into Asia and other parts of the Old World tropics soon after the discovery of Brazil, but did not become an important crop in America until after the Civil War (1866).

Among other legumes of economic importance may be mentioned the following:

Cowpeas (*Vigna catjang* Walpers, and *V. sinensis* Endlicher), two species used for forage and green manure, and the seeds for food. Since the cotyledons are raised above ground when the seed germinates, it is botanically a bean and not a pea as its common name would imply. In China it is called, more appropriately, "black-eyed bean." Its flower differs from that of *Phaseolus* in not having a spiral keel, and from that of *Dolichos* in having a style-beak which extends beyond the lateral stigma. The plant is native in Persia and India. The name cowpea is more properly restricted to *V. sinensis*, the other species, commonly called *catjangs*, has smaller pods and seeds than *V. sinensis*, and the pods remain erect when ripening, whereas the ripe pods of the true cowpea are pendent when ripe. Cowpeas are extensively cultivated in China and in the southern United States. They are botanically closely related to the following.

Dolichos.—Only three of the more than 50 species are grown in America. The Hyacinth Bean (*D. Lablab*) is a tropical annual climber. In the tropics its pods and seeds are eaten, but in America it is grown for ornament. The Australian Pea (*D. lignosus*)

is a tender evergreen climber, that grows well in Arizona and southern California. *D. biflorus* is used as a forage plant in India.

Cajanus or Pigeon Pea (*Cytisus Cajan*), an African legume cultivated in the tropics for its edible seeds, and in the West Indies as food for both men and stock.

Dalbergia, a genus having about 100 species of trees, shrubs, and vines, found in both the old and new world tropics. One species (*D. Sissoo*) is a good timber tree in India. The timber of one species is known as rosewood, but this name is also applied commercially to the wood of several other kinds of trees.

Logwood (*Haematoxylon campechianum*), a tree native in Central America, and grown in the West Indies. The wood is shipped in the form of blocks and logs, whence the name. From the wood a coloring substance is extracted which is used as a microscopic stain, in the manufacture of ink, in dyeing, and slightly in medicine.

Lupines (*Lupinus*).—The genus has some 300 species, and is very variable as a garden ornamental. Some species are valued for green manure. The blue, white, yellow, and variegated flowers are borne on showy terminal racemes, making a beautiful garden plant. Some species are annuals, some perennials. *Lupinus arboreus* is a shrub 4–10 feet high.

CHAPTER XXX

POLYPETALOUS DICOTYLEDONS (CONTINUED)

ORDER, Geraniales

This and the following order (*Sapindales*) include trees, shrubs, and herbs. In both orders the floral parts are usually in fives, with two whorls of stamens, usually five in each whorl. The two orders differ in details as to the ovule.

GERANIUM FAMILY

The Geranium Family (*Geraniaceae*), which gives the name to the order, contains the wild geraniums, or Cranesbills[1] common in North America, the cultivated house-plant and garden-plant (Fig. 182), commonly called Geranium, but belonging to the genus *Pelargonium*, indigenous to South Africa, and about eight or ten other genera, with some 450 species widely distributed in temperate and tropical zones. There are numerous horticultural varieties of *Pelargonium*, and their characteristic odor is due to an aromatic oil secreted by glandular epidermal hairs.

FLAX FAMILY

The most important family of this order, economically, is *Linaceae*, containing *Linum usitatissunum*, the cultivated Flax (Fig. 437). There are ten or twelve known genera and as many as 150 species of herbs and shrubs, widely distributed. About 25 species are growing without cultivation in the United States. There are several, more or less distinct, forms of the cultivated flax, a few being considered separate species by some botanists. The seeds of the plant yield the commercially valuable linseed (*i.e.*, *Linum*-seed) oil, and the long bast fibers of the stalk (Fig. 438) are the raw material of which *linen* (from *Linum*) is made. The English words lint and line are also from *Linum*. Flax has

[1] *Geranium* is from the Greek word γέρανος (geranos), meaning, a *crane*, from the fancied resemblance of the long beak-like fruit to a crane's bill.

been cultivated, especially for its fibers, from prehistoric times, but the form earliest cultivated was probably *L. angustifolium*. The North American Indians used the fiber of *L. perenne*, which has three stalks growing from a perennial root. The ancient Hebrews and Egyptians wore linen 4000–5000 years ago, the latter using it also for mummy cloth. The latter fact is confirmed by a microscopic examination of the cloth. It is known that the

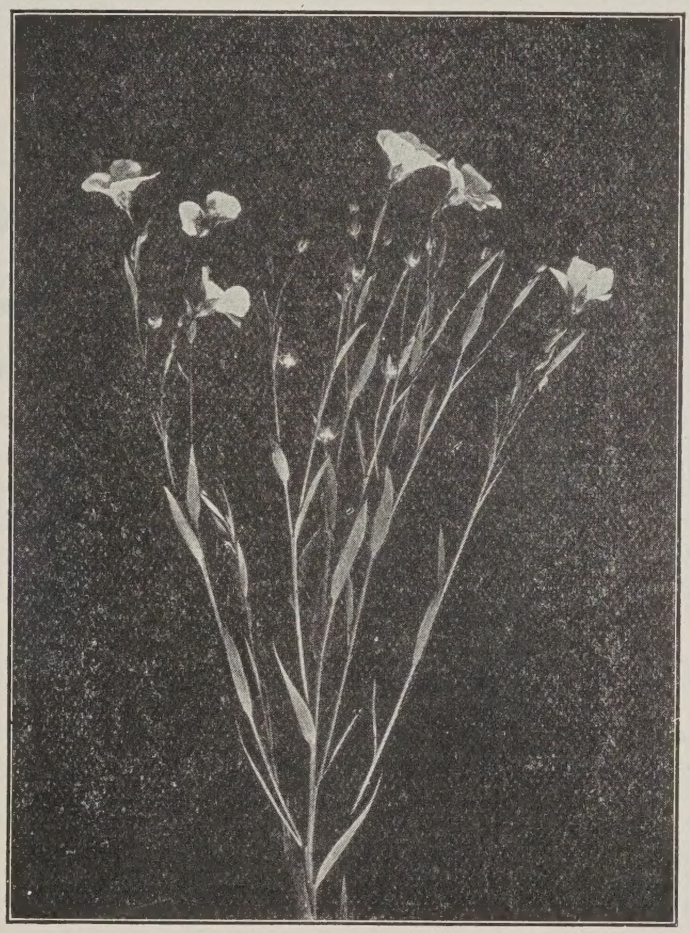


FIG. 437.—Common flax (*Linum ustitatissimum*). (After Robbins.)

Greeks were importing linen from Colchis the land of the Golden Fleece (between the Caucasus and Armenia), several hundred years before Christ. The people of Colchis were noted for their manufacture of linen. The fact that the common name for linen is so widely different and unrelated in different countries also indicates a very ancient origin of its cultivation.

The flowers, in corymbs or panicles, are regular and symmetrical. There are 5 sepals and 5 petals, and the filaments of the

5 stamens are united (monadelphous) at the base. The flowers are normally self-pollinated. The fruit is a capsule or pod formed by the union of 5 carpels, each cell containing two mucilaginous, flattened seeds. By false partitions the pod may become 10-celled.

Many of the species are perennial, but the fiber-flax is cultivated as an annual, and the stems attain a height of 20–40

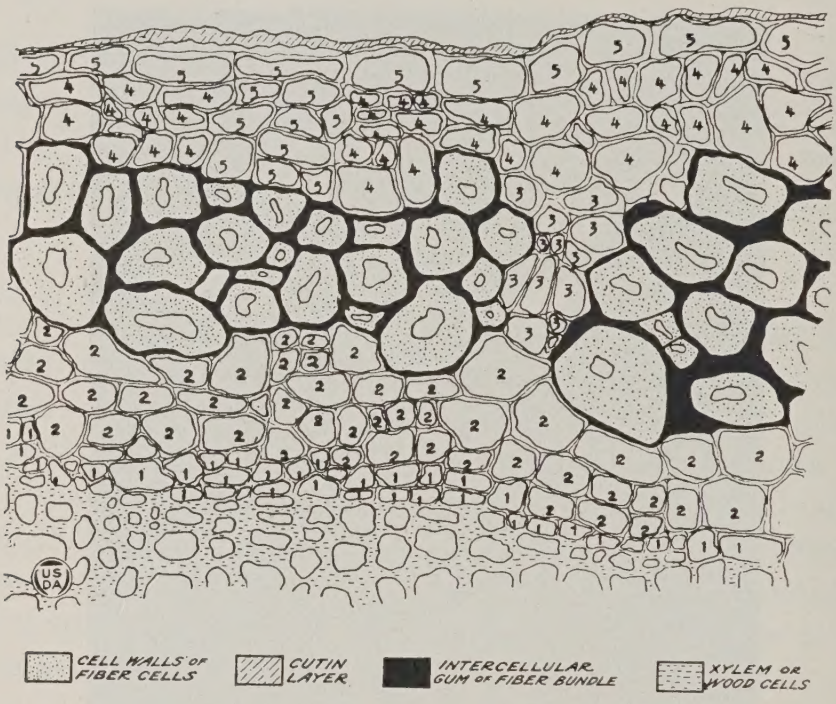


FIG. 438.—Flax (*Linum usitatissimum*). Portion of a cross-section of the stem. The numbers indicate the order in which the tissue is destroyed by the enzymes in retting. 1, cambium layer; 2, phloem parenchyma; 3, parenchyma between the bundles; 4, outer parenchyma; 5, epidermis. Note that the thickness of the intercellular gum between the thick-walled fiber-cells is greater than the thickness of the cell-walls of the adjacent parenchyma. (After R. L. Davis. U. S. Dept. Agr. Dept. Bull. No. 1185.)

inches, branching only at the top. The narrow, lance-shaped leaves are alternate and sessile and with no stipules or only small ones.

The blue-flowered *Linum perenne*, the red flowered *Linum grandiflorum*, and others are cultivated in gardens for their flowers. The globular seed-capsules are five lobed and about the size of a large edible pea seed.

The varieties of seed-flax, grown extensively in the Northwestern United States, are distinct from the varieties of fiber-

flax, though there are intergrading forms. Fiber-flax is grown only in limited areas in the United States, but is grown extensively in Russia, Caucasia, and other European countries. Its main stems are longer than those of the seed-flax, and its yield of seed per acre is much less than that of the seed-flax. The latter produces fibers as well as seed, but they are not as long nor of as good quality as the fibers of the fiber-flax plants.

The fiber-flax plants, growing in the field close together, usually have only one straight stem, averaging about 30 inches high, and branching only at the top to form the flower panicle. These stems are only about one tenth of an inch thick. The shade resulting from the thick stand prevents the development of side branches which would cause uneven places in the fibers which form part of the fibro-vascular system in the cortex, and would send out branches into the lateral stems should they develop.

In harvesting, the flax plants are usually not cut off but are pulled up so as to insure the longest possible fibers. The fibers are prepared by a series of processes as follows:

1. *Rippling*, in which the plants are drawn through upright forks to remove the leaves and fruit capsules.

2. *Retting*, or, as the word means, soaking and rotting. By this process the fibers are loosened from the surrounding tissues which decay more rapidly.

3. *Breaking*, by which the decayed tissue is broken into small pieces.

4. *Scutching*, by which the broken tissue is removed, leaving only the flax fibers.

The fibers are held together in the stem by a substance (intercellular gum) composed in large part of *calcium pectate*. In retting this substance is made soluble by the action of an enzyme, *pectinase*, secreted by bacteria in the water. In *dew-retting* the flax "straw" is spread out on the ground, exposed to dew and sun. In this process, according to Behrens, the active enzyme is secreted by filamentous fungi.

When properly retted, the fibers are 12–36 inches long. They are used in making linen cloth of all kinds, seine twine, fish lines, and thread for book-binding, shoe-making, and other sewing. Since the fibers are better conductors of heat than is cotton all linen goods are cooler to the touch than are cotton fabrics.

SPURGE FAMILY

Another species of great economic importance is the Castor-oil plant (*Ricinus communis*), of the Spurge Family (*Euphorbiaceae*). There is only one species of the genus, although hundreds of forms are known. All forms grow as annuals in the temperate zone, but some forms grow as perennials in warmer climates. The plant is monoecious, with apetalous flowers, the pistillate

FIG. 439.—*Ricinus communis.* Inflorescence in ripe fruit.

above the staminate in a somewhat panicled raceme (Fig. 439). The stamens are branched. The fruit is a spiny capsule and the seeds (3 in each capsule) contain a poisonous substance, *ricin,* and yield the castor-oil of commerce—used not only as a medicine, but also as a lubricant, especially for aeroplane motors. The seeds of different varieties vary greatly in size and in color-pattern (Fig. 440). In certain parts of India, streets and railway

stations have been lighted by an illuminating gas made from castor-oil.

The native home of *Ricinus* is tropical Africa. The plant readily escapes from cultivation and becomes established as a weed in waste places. It varies greatly, many varieties having been described. This may be an evidence of its antiquity as a cultivated plant. Seeds have been found in ancient Egyptian tombs, and the plant is mentioned by Theophrastus[1] and by Dioscorides.[2]

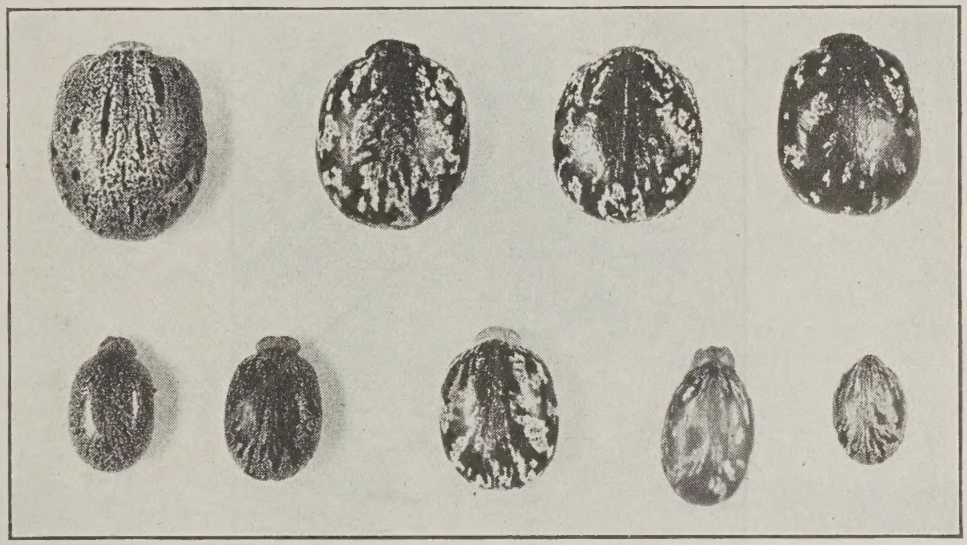


FIG. 440.—*Ricinus communis.* Variation in size and color pattern of seeds of different varieties. The appendage at the upper ends of the seeds (around the micropyle) is the *caruncle.* Natural size.. (After O. E. White.)

RUBBER

Commercial rubber (*Caoutchouc*) is derived from several species of *Euphorbiaceae,* but chiefly from *Hevea brasiliensis* and *H.*

[1] THEOPHRASTUS has been called the "first of real botanists in point of time." He was a pupil and successor of Aristotle, as president of the Lyceum, 322 B.C. His books *On the history and causes of plants* are the earliest botanical works now in existence. He was born on the Island of Lesbos (now Mitylene) 370 B.C., and died at Athens, 285 B.C.

[2] DIOSCORIDES was born at Anazarbius, in Sicily, and flourished about 64 A.D. He was a physician who travelled widely in Asia Minor, presumably botanizing where he went. He was the author of what has been called perhaps the most assiduously studied textbook of botany ever written. He was the supreme botanical authority for over 1600 years. His work was pharmaceutical in nature, and he is credited with having been one of the first to recognize "most of the more familiar natural families of plants."

guyanensis, natives of South America (Figs. 441, 442, and 443). The commercial demand for rubber enormously increased with the introduction of the automobile and the general use of rubber for the tires of all manner of vehicles, for rubber heels, shoes, coats, and several thousand other uses. In fact, the rubber industry is now the fourth largest industry in the United States, consuming about two thirds of all the rubber sold. Four fifths

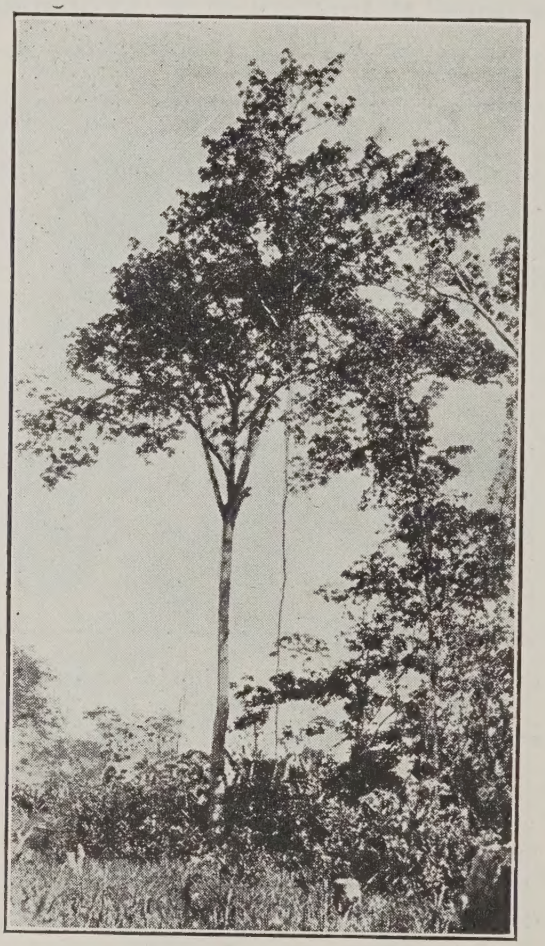


FIG. 441.—Para rubber tree (*Hevea brasiliensis*), near Para. (From Arboretum Amazonicum.)

of this rubber is made into automobile tires. About 5000 square miles are planted to Para rubber (*Hevea brasiliensis*), besides the supply that is drawn from wild trees.

It is interesting to know that the development of the large rubber plantations in Ceylon, Southern India, and the Malay Peninsula are the result of the work of a botanic garden—the Royal Botanic Gardens at Kew, England. In 1875 expert

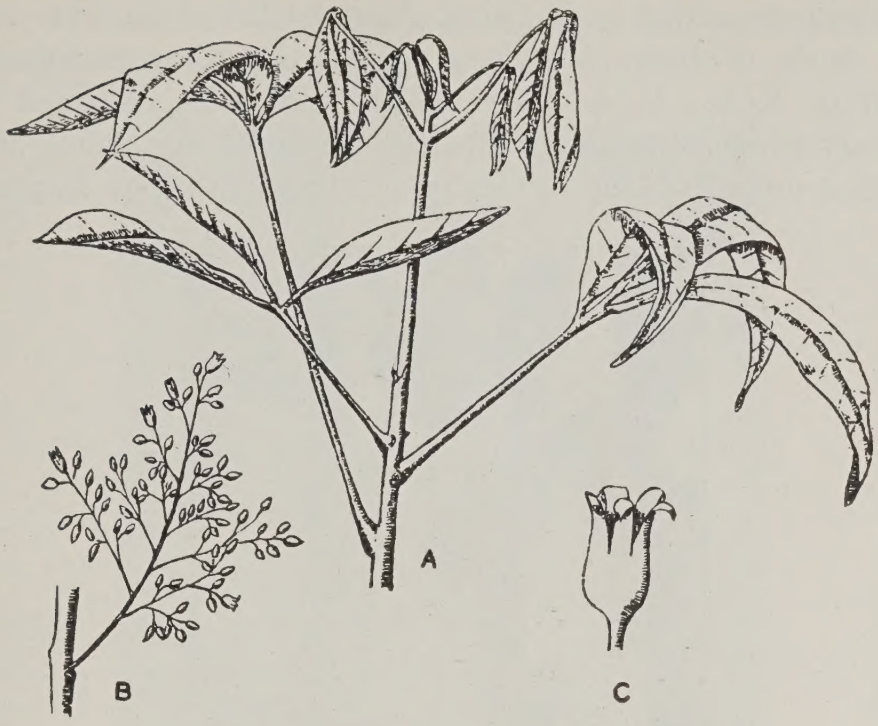


FIG. 442.—Hevea brasiliensis. *A*, young shoot; *B*, inflorescence; *C*, flower. (After R. H. Lock.)

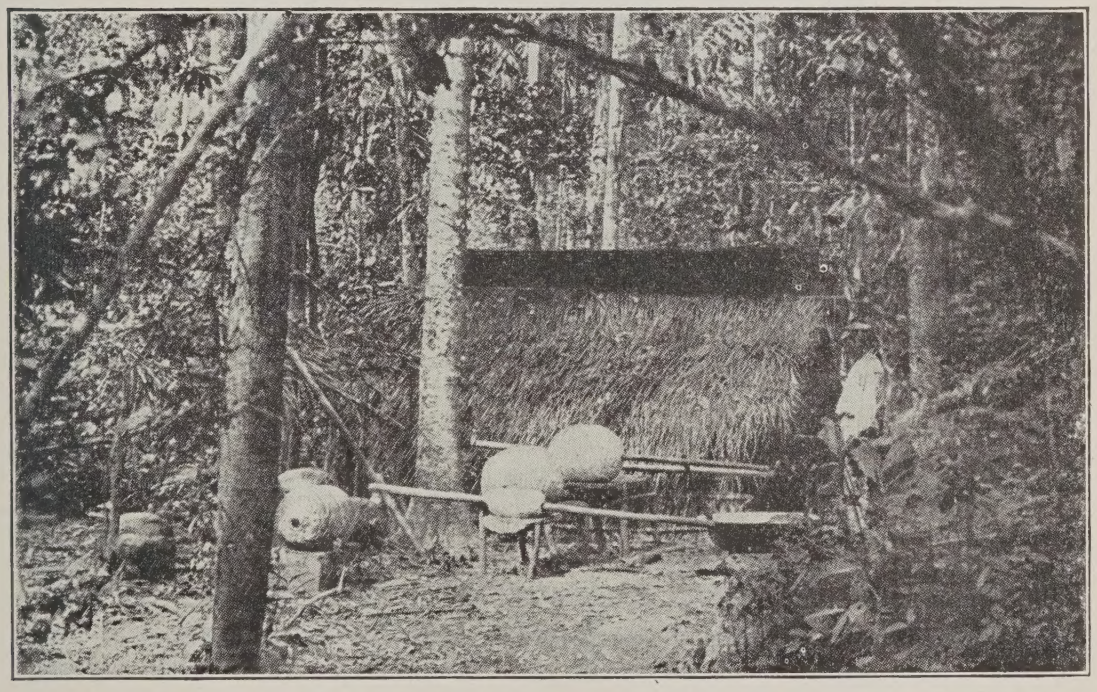


FIG. 443.—Para rubber. "Biscuits" ready for shipment. They are formed by pouring latex on the pole or "paddle" as the latter is rotated over a fire. (From R. H. Lock.)

collectors succeeded in shipping about 70,000 of the very short-lived seeds of *Hevea brasiliensis* from the Amazon forests of Brazil to Kew. From these seeds there were obtained 1000 seedlings which were shipped to the countries mentioned above, the chief nursery being in Ceylon. The plants were shipped in

FIG. 444.—Central American rubber (*Castilla elastica*). Pistillate flowers (on the two branches at the left) and staminate flowers (at the right). (After O. F. Cook. U. S. Dept. Agr. B. P. I. Bull. 49.)

Wardian cases[1] in 1879, and these plants and their descendants became the source of most of the Para rubber of commerce. As

[1] Wardian cases consist of a soil-bed covered with a closed but ventilated glass hood, being, in reality, a miniature greenhouse. Plants will keep in this case for weeks or even for months without watering, or open exposure to air. The case was devised by Mr. N. B. Ward, of England, about 1833, in order to overcome the difficulty of shipping ferns and other plants to and from tropical countries—especially across the equator. (Ward, N. B. *On the growth of plants in closely glazed cases.* London, 1842.)

late as 1913, about 40 of the original trees were still growing in Ceylon, having reached a girth of nearly ten feet.[1]

FIG. 445.—*Castilla elastica*, Native method of tapping. A somewhat similar method is used with *Hevea*. (After O. F. Cook. U. S. Dept. Agr. B. P. I. Bull. 49.)

[1] Species of Manihot (ceara rubber) and Sapium, of the Euphorbiaceæ, are sources of commercial rubber, of minor importance, as are also *Castilla* (*Castilloa*) *elastica* (Central America rubber tree) (Figs. 444 and 445), and *Ficus elastica* (Assam rubber), both of the Moraceæ (Urticales); some ten or twelve species of the Dogbane Family (Apocynaceæ) and two species of the milkweed Family (Asclepiadaceæ) (Gentianales); and guayule (*Parthenium argentatum*), of the Compositæ (Campanulales). (Lock, R. H. *Rubber and rubber planting.* Cambridge and New York. 1913. pp. 16–17.)

The roots of *Manihot utilissima* (bitter cassava—a poisonous species) are the source of tapioca and *farinha*. The roots of a related, non-poisonous species (*M. aipi*—sweet cassava) are used as a vegetable food in tropical countries.

RUE FAMILY

The Rue family (*Rutaceae*) comprises trees, shrubs, and rarely herbs, all characterized with simple or compound leaves dotted

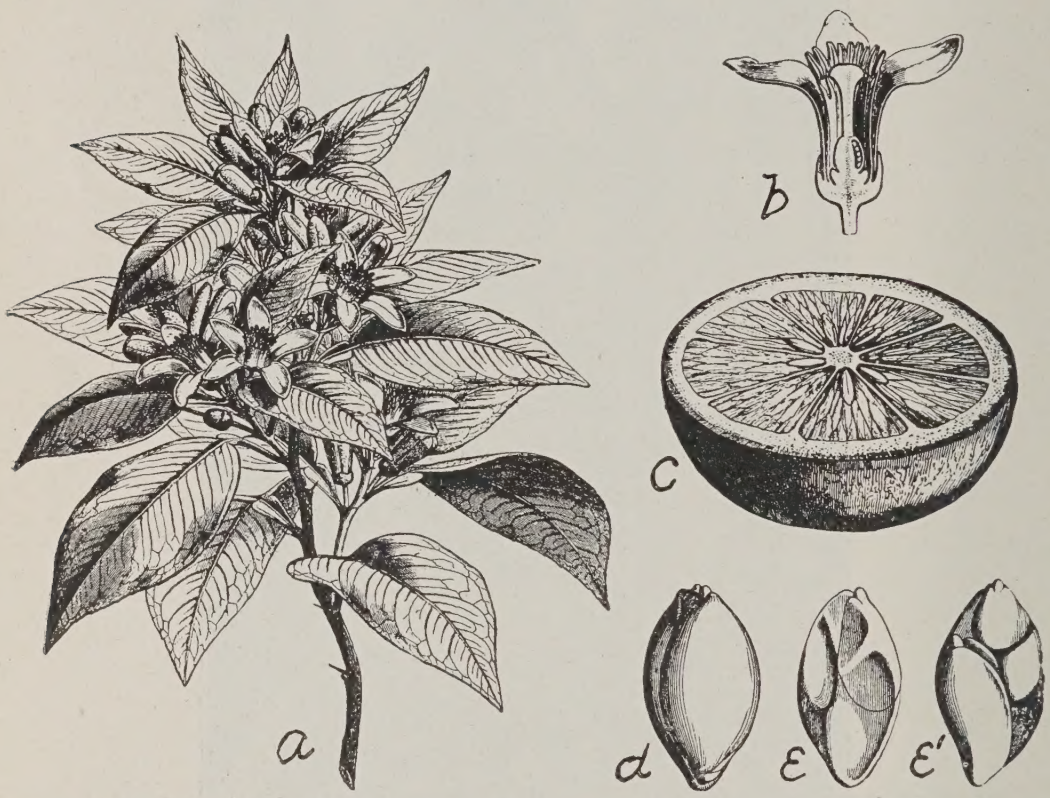


FIG. 446.—Orange. Flowering branch, flower in longitudinal section, fruit in cross-section, seed (with seed coat removed), and embryos showing polyembryony. (After Baillon.)

with sunken glands that secrete an aromatic volatile oil. In some genera the leaves are opposite, in others alternate. They may be simple (some species of *Haplophyllum*), pinnate (*Xanthoxylum, Ptelea*), reduced pinnate in the orange (*Citrus Aurantium*), or twice or thrice pinnatifid, as in the common Rue (*Ruta graveolens*). The 2–5 pistils may be separate, or combined to form a compound ovary of as many cells, raised on a glandular disc formed by a prolongation of the receptacle (Fig. 446). The sepals and petals are more or less united in *Citrus*. The fruit

may be a *berry* (orange, lemon, and other species of *Citrus*), a *capsule* (prickly-ash), or a samara (*Ptelea*).

The Rue family comprises some ten genera with about 750 species, of wide distribution in temperate and tropical regions, chiefly in the eastern and southern hemispheres. In the northeastern United States the family is represented by three genera, as follows:

1. *Xanthoxylum*, or Prickly-ash, having dioecious flowers, 3–5 separate ovaries, and the fruit a fleshy pod or capsule. The northern Prickly-ash or Toothache Tree (*X. americanum*) ranges from Quebec to Virginia and westward to Kentucky, Missouri, eastern Kansas and Minnesota, flowering in April and May. The southern Prickly-ash (*X. Clava-Herculis*) inhabits stream borders along the coast from Virginia southward to Florida and westward to Texas, flowering in June.

2. *Ptelea* (Hop-tree, Shrubby Trefoil), with polygamous flowers, a two-celled ovary, and the fruit a two-seeded samara or key, with the wing extending all the way around (really two-winged). The one species, *Ptelea trifoliata*, which is a tall shrub, ranges from Long Island westward to Ontario and Minnesota, and southward to Florida. The bitter fruit is said to be used as a substitute for hops.

3. *Ruta* (Rue), herbs or undershrubs with alternate divided leaves, perfect flowers, ovary 4–5 lobed, forming a several seeded capsule. The calyx persists in the fruit. Only one species (*Ruta graveolens*), formerly occurring only under cultivation in the northeastern United States, has now become established in pastures in Vermont, Virginia, and probably elsewhere. The "gas plant" (*Dictamnus*) also belongs in this family.

The economically most important genus of the Rutaceae is *Citrus*, which includes the orange, lemon, lime, grape-fruit, tangerine, kumquats, and other citrus fruits of commercial value.

ORANGES

The oranges of commerce are all species of *Citrus*.[1] The genus *Citrus* belongs strictly to the Old World, not being found wild in either North or South America.

[1] Alphonse De Candolle (Origin of cultivated plants. London, 1904. p. 184) gives the following interesting information as to the origin of the

The roots of *Citrus* possess no root-hairs, being dependent, therefore, on mycorhizas for the absorption of water from the soil (*Cf.*, p. 214). In shallow soils the absorbing roots lie near the surface, but in deeper and well-aerated soils they are distributed at various levels from eight inches to three feet or more. There is normally a large tap-root, but this does not appear to be essential and is often removed when young trees are transplanted.

With the single exception of *C. trifoliata*, all species and varieties are evergreen, the leaves of the preceding year remaining on the tree until the leaves of the current year have expanded. The leaves may remain on the tree and active from about 15 months (on small, fruit-bearing branches) to 3–4 years (on strong vegetative branches). Leaves growing on the trunk may remain on still longer, but are commonly removed in orchards to reduce the loss of water by transpiration (*Cf.*, p. 123).

With the exception of the navel orange and one variety of Lemon (Eureka), most of the species of *Citrus* bear thorns which are modified branches growing in the axils of leaves. These thorns not only increase the difficulty of picking the fruit, but often cause injury to the fruit itself as the trees are swayed by heavy wind.

The leaves are thickly dotted with glands of various sizes which secrete an essential oil. These glands occur in the epidermal portion of practically every organ except the roots—appearing even in the embryo. The persistent leaves appear to be simple but are really compound, the "blade" being the terminal leaflet of a tri-foliolate, pinnately compound leaf. The joint

---

word "orange." There was a Sanskrit name for the orange—*nagarunga*, *nagrunga*. It is from this that the word orange came, for the Hindus turned it into *narungee* (pronounced, *naroudji*) according to Royle, *nerunga* according to Piddington; the Arabs into *narunji*, according to Gallesio, the Italians into *naranzi*, arangi, and in the mediaeval Latin it was *arancium*, *arangium*, afterwards *aurantium*." The English form of the word came through the Moors by way of Spain. It became *naranja* in Spanish, *arancio* in modern Italian, *oranger* in French, *orange* in English. As usual the specific name is the Latin form. The word was probably originally applied to the bitter orange, before the sweet orange was commonly known.

Since the odor of the fruits of the citron (called *Citrus Medica*, because early imported into Rome from *Media*) suggested the odor of the wood of *Cedrus* (cedar) the Romans erroneously supposed the fruit came from that tree. This undoubtedly explains the origin of the generic name, *Citrus*.

between the winged petiole and the base of the "blade" is evidence of the compound nature of the leaf. In the trifoliate orange, *Citrus trifoliata*, the leaves have the full compliment of three leaflets. The leaf-margin varies from entire to crenate or toothed, depending on the species, and there is a marginal oil gland in the angle of each crenation. These marginal glands also occur when the margin is entire.

The flowers of *Citrus*, borne in cymes on shoot-spurs of the current year's growth, have a calyx of 3–5 green sepals, a corolla of 4–8 rather fleshy, white, waxy petals, which contain oil glands, and 20–60 stamens with the lower portions of the filaments united. The thick style is terminated by a knob-like stigma which secretes a white mucilaginous substance. At the base of the corolla are glands that secrete a watery nectar. The stamens produce generous quantities of yellow pollen, except that the flowers of the Washington navel orange do not bear pollen, and in the Eureka lemon most of the pollen aborts and is therefore of no value in pollination.

While certain varieties of orange require pollination in order to set fruit, Ikeda[1] has shown that other varieties will set fruit either with or without pollination. Fruits formed without pollination are called *parthenocarpic* fruits, the phenomenon is called *parthenocarpy*. Ikeda has also shown that cross-pollination between certain varieties results in the dropping of the flowers of young fruit, and that some varieties are normally parthenocarpic. It requires about 72 hours for fertilization to be complete after pollen has reached the stigma. In the Washington navel and Satsuma oranges the embryo-sac normally disintegrates, but in exceptional cases it persists, fertilization takes place, and the ovule develops into a seed with embryo. This accounts for the rare occurrence of seeds in navel oranges.

Polyembryony.—In most plants a seed normally contains but one embryo, the occurrence of more than one embryo in a seed (*polyembryony*) being comparatively rare. In the genus *Citrus*, however, polyembryony is a common occurrence, a single seed often containing from two to ten distinct embryos. Strasburger reported thirteen seedlings from a single seed. One of these

[1] Ikeda, T. On the parthenocarpy of citrus fruits. Jour. Sci. Agr. Soc. Tokyo. No. 60, p. 19–34; No. 63, p. 5–17. 1904.

embryos, in most if not in all cases, arises in the normal way from the fertilized egg-cell in the embryo-sac, and therefore contains hereditary material from two parents. As is usual in such cases, the offspring of this plant will not breed true in the second and subsequent generations.

The remaining embryo or embryos arise as outgrowths of the nucellus (which surrounds the embryo-sac) by a process of "budding." They, therefore, contain hereditary material from one parent only—the pistillate parent, and seeds from them will breed true in the second and subsequent generations—provided, of course, that the strain was pure to start with.

The occurrence of polyembryony introduces serious complications in breeding, for it is difficult, if not quite impossible, to tell, when several seedlings arise from a germinating seed, which one of them came from the fertilized egg-cell, as the result of the cross, and which arose vegetatively from the nucellus.[1]

The fruit of Citrus is considered by Bonavia[2] to represent (morphologically) two whorls of modified leaves, the outer one being metamorphosed to form the rind, and the inner to form the carpels, each carpel being represented by one of the sections into which an orange or other citrous fruit may be so easily separated. The number of these sections is indefinite, even in the same variety.

The small, imperfectly developed little fruits in the apical end of a navel orange are formed by supernumerary whorls of carpels, a phenomenon analagous to what often takes place in the formation of a double flower.

The juice-bearing vesicles or sacs of the citrous fruit are multicellular, and are attached by one end to the carpel. Each one is supplied with a fibrovascular bundle which extends from the stalk up through the white spongy inner tissue of the rind. Bonavia considers them homologous with the oil glands of the rind.

About 85% of an orange is water, about 14% is organic matter, of which less than ½% is ash. There is a total of about 10%

[1] Not all supernumerary embryos arise by budding from the nucellus. In some species they may arise from the fertilization of the fusion-nucleus in the embryo-sac by the second sperm-nucleus (*Cf.* pp. 346 and 352). This does not appear to be the case, however, in *Citrus*.

[2] Bonavia, E. Oranges and lemons of India. Chapter XIV. London 1888.

of various sugars. Navel oranges contain about 1% citric acid, and lemons about 7½%.

SPECIES AND VARIETIES OF CITRUS

The species and varieties of *Citrus* readily cross, and this fact renders their classification rather difficult, so that there is no general agreement among systematic botanists as to their classification. The common species in commerce are included in the following table.[1]

Citrus
1. *trifoliata*, the deciduous orange.
2. *bergamia*, Bergamot orange.
3. *sinensis*, common sweet orange.
4. *Aurantium*, sour, Seville, or bitter orange.
5. *nobilis*, King orange.
   - *a.* var. *deliciosa*, Mandarin or kid-glove orange, Tangerine.
   - *b.* var. *unshiu*, Satsuma orange.
6. *japonica* (*Fortunella japonica*), kumquat.
7. *Medica*, citron of commerce.
8. *ichangensis*.
9. *grandis* (*C. Aurantium decumana*), grape-fruit (pomelo), Shaddock.
10. *mitis*, Calamondin orange.
11. *Limonia*, lemon.
12. *aurantifolia*, lime.

Citrus trifoliata, a native of China and Japan, does not bear an edible fruit, and is cultivated chiefly as an ornamental plant, and (especially in Florida) as a stock on which to bud the edible varieties, nearly all of which do well on trifoliate stock, though somewhat dwarfed in the process. It is hardy as far north as New York City. Hybrids between this form and the common orange are called *citranges*, and several varieties of citrange are hardy north of the belt of successful orange culture. *C. trifoliata* differs from all other species that have been referred to *Citrus* by having deciduous leaves, and in other botanical characters which led Rafinesque to refer it to another genus, *Poncirus* (French, *poncire*, citron). The synonym is *Poncirus trifoliata*.

Citrus bergamia Risso., a small tree, is grown commercially in Italy (Calabria) and elsewhere in Europe as the source of

[1] Compiled from Coit, J. Eliot. Citrus fruits. New York. The Macmillan Co. 1917. p. 43; and Stand. Cyclop. Hort. **2**: 780–785. 1919.

bergamot oil. It is sometimes grown in California as a hedge or a specimen plant in gardens. The pyriform fruits are pale yellow when ripe, thin skinned, very seedy, and with acid juice.

The *sweet orange* (*C. Aurantium sinensis*, Linnaeus) was found only as a cultivated plant in India by Sir Joseph Hooker. The weight of evidence seems to point to southern China and Cochin-China as its native home, from which region it may have spread into eastern India near the beginning of the Christian era. Its seeds are distributed by birds and by man. There is no special name for this orange in Sanskrit and this would indicate that its cultivation was introduced into India at a late date. It was not known to the ancient Greeks nor to the Hebrews in Palestine, nor to the Romans. It is cultivated in nearly all tropical and sub-tropical countries. A variety with reddish pulp is called "blood orange."

Citrus Aurantium Linnaeus is used by some botanists to designate only the sour or bitter Seville orange, *Citrus sinensis* being used for the sweet orange.

The *bitter orange* (*C. Aurantium bigaradia*, of Hooker) was known in eastern India, and probably as a wild fruit, before the fall of Rome, and was cultivated in Arabia in the latter part of the ninth century. De Candolle says the Crusaders found it in Palestine. It was introduced into Spain by the Arabs, is largely used in making marmalade, candied orange peel, and a bitter tincture. Since the bitter orange is more resistant than some other varieties to foot-rot and gum disease it is largely used in California as a stock on which to work (*i.e.*, graft) various kinds of citrous fruits. The seeds are obtained largely from Florida, where the species is naturalized.

Citrus nobilis Lour.[1], or King orange, bears leaves with margined or narrow winged petioles, and medium sized fruits with hollow pith and very loose peel which may readily be removed without squeezing out the juice—whence the common name, "kid-glove" orange. The seeds are commonly green within. The *Mandarin* oranges with depressed-globose, orange-yellow fruit, and the *Tangerines*, of similar character but red-orange in color, are forms of *C. nobilis*. In 1897 Swingle[2] crossed the

[1] Loureiro, Juan. 1715–1796. A Portuguese missionary to China.

[2] Webber, Herbert J. and Swingle, Walter T. New Citrus creations of the Department of Agriculture. Year Book, Dept. Agr. **1904**: 235. 1905.

Dancy tangerine with the Bowen grapefruit, and obtained a hybrid having the structural characters of the tangerine, the acid juice of the grapefruit (though much milder), and a size intermediate between the fruits of the two parents. Webber called this hybrid the Sampson *tangelo* (tangerine + pomelo). The Thornton tangelo is a cross between a tangerine and a Florida grapefruit.

The Satsuma orange (var. *unshiu*) is a dwarf tree of spreading habit of growth, without spines, and bearing deep-orange-colored fruit with orange-colored pulp. Structurally it resembles the tangerine. It was introduced into Florida from Japan in 1876, and when budded on *trifoliata* stock is hardy in the Gulf states far beyond the northern limits of the sweet orange. In Alabama, Satsuma oranges become edible some weeks before the skin turns from green to orange, and, in preparation for market, the chlorophyll is artificially destroyed by the exhaust gas given off by a gasolene engine or by the incomplete combustion of kerosene.

Citrus japonica Thunberg (=*Fortunella japonica* Swingle), is an evergreen shrub, with small, round, oval, or spindle-shaped fruits which are eaten "skin and all," except the seeds. Since the ovary is few-celled, with only two ovules to a cell, this form was removed from the genus *Citrus* by Swingle, and referred to the genus *Fortunella*[1]. Four species are recognized by Swingle: *F. margarita* (oval, or Nagami, Kumquat), the form first introduced by Fortune; *F. japonica* (round, or Marumi, Kumquat), much grown for ornament; *F. crassifolia* (Meiwa Kumquat), introduced into the United States from Japan; and *F. Hindsii* (Hongkong wild Kumquat). Of the last species, Swingle says: "It is the most primitive of the true citrus fruits, and doubtless the species of *Citrus* have evolved from such a plant."[2]

Citrus Medica Linn. It is from the rind of this species that the candied citron of commerce is made (*Cf.* p. 784). It grows as a small tree or shrub, with long, thorny branches, wingless petioles, and leaf-blade not jointed with the leaf-stalk. The flowers occur in terminal panicles or in clusters in the leaf-axil. The large petals are white above and purplish or reddish purple

[1] After Robert Fortune, who introduced the fruit into Europe from Cochin-China in 1846.

[2] Standard Cyclop. Hort. **3**: 1270. 1919.

underneath; there are 30–40 stamens, the style commonly persists, and the lemon-yellow fruit has little pulp, but a very thick, fragrant rind. This species is, in places, known as "Adams apple." It is propagated by seeds or by layering. It is in common cultivation in Corsica and the Mediterranean region generally.

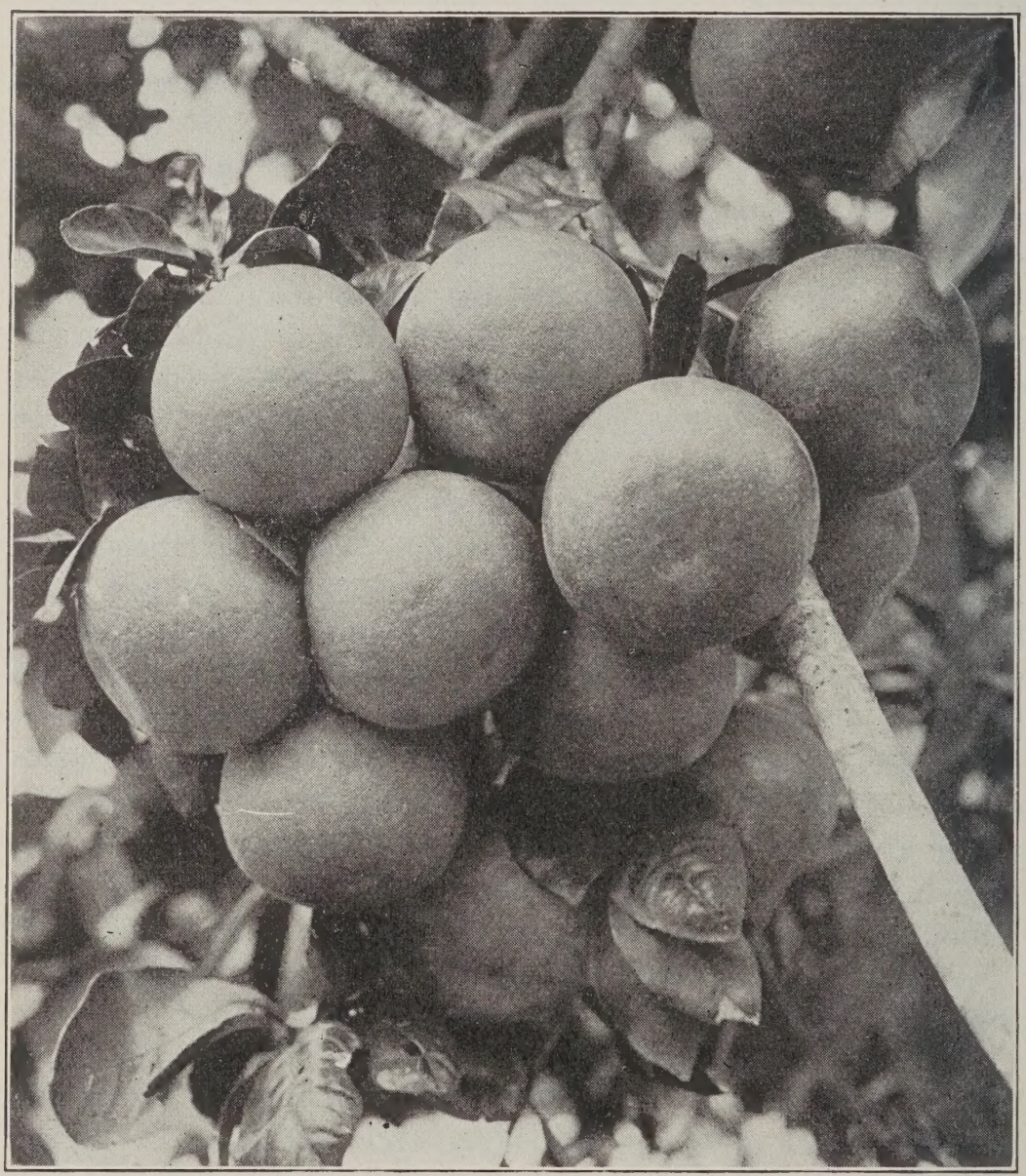


FIG. 447.—Cluster of Grapefruit (*Citrus grandis*), grown in Florida.

Citrus ichangensis Swingle is found native in the highlands of south-western China. It is very resistant to cold, grows at an altitude of 3000–5000 feet, and extends farther north than any other evergreen *Citrus*. It is thought that it may prove of

value in breeding experiments having for their object the production of a hardy substitute for the lemon.

Citrus grandis Osbeck (*C. decumana* Linnaeus) was called by early Dutch traders Pompelmoes (*i.e.*, pumpkin-citron), doubtless from its large size. The Japanese called it Pomplemus. Other common names are Pompoleous, Pumelnose, and Pomelo. This species is thought to be a native of the Malay Archipelago. It was introduced into India and Ceylon by way of Java in the 17th century. There are two well-marked groups or types; one, with thin skin and mildly bitter juice, is now common in the markets under the trade name "grapefruit"[1] (Fig. 447). Nearly all the commercial varieties of grapefruit have originated as seedlings in Florida. The second type, the Shaddock, named after Capt. Shaddock, who first brought this species to the West Indies, has a very thick skin and very bitter juice. It is quite inedible.[2]

Citrus mitis Blanco, the Calamondin orange, is a small tree native in the Philippine Islands, and introduced into the United States from Panama by the U. S. Department of Agriculture. This form is very hardy and, on account of the very acid pulp, the fruit is of value in cooking and in making ale.

Citrus Limonia Osbeck (=*C. Medica Limon* Linnaeus, = *C. Limonium* Risso) derives its specific name from the Arabic word for lemon—limun. This is the lemon of commerce. It is

[1] Watt says: "The cells of the pulp are very large and naturally separate from each other—a peculiarity that has led some people to speak of it as the "Grape Fruit" or "Grape Orange." A more reasonable explanation of the name grapefruit would be the manner of growth of the fruit in clusters which resemble bunches of giant grapes.

[2] Merrill and Lee (Am. Jour. Bot. **11**: 382–384, June, 1924) call attention to the fact that Burman, in 1755, in his *Index Universalis Herbarium Amboinense*, called the East Indian shaddock *Aurantium maxima*. Linnaeus had previously called it *Citrus Aurantium* var. *decumana*, and finally *C. decumana*. Since Burman's *specific* name, *maxima*, antedates all others it is the valid name according to all codes of botanical nomenclature. As Merrill and Lee point out, the species includes at least two distinct forms—the thick-skinned, inedible East Indian shaddock, and the West Indian and American-grown grapefruit of commerce. In order to make the nomenclature more definite, they propose the formation of a botanical variety, *Citrus maxima* var. *uvacarpa* for the grapefruit, leaving the binomial, *C. maxima*, to designate the shaddock.

a small tree, the branches armed with short, thick thorns, the petioles wingless or with only narrow margins, and with joints at both ends. The large flowers are solitary, or in small axillary clusters, with petals colored similarly to those of *Citrus medica*, to which it has been referred as a variety by some authors. The peel is noticeably dotted with glands. It is cultivated very generally in tropical and subtropical regions, but is very sensitive to cold; it does well in California and Florida. The fruits are usually gathered while green, or even before they are full-grown, and ripened in curing houses. There is a considerable number of commercial varieties with the fruits differing in shape, size, number of seeds, acidity, thickness of peel, and other characters. The *Ponderosa* variety has fruits that sometimes weigh as much as 2½ lbs.

Lemons are subject to a physiological disturbance, which results in the destruction of the internal tissues of the fruit, usually at the "blossom end" (opposite the stem-end). By growers and dealers this trouble is called blossom-end decay, yellow tip, dry tip, etc. The severity of the disease varies from year to year, fluctuating from not more than 2% to as much as 60% of the crop in a given grove. The characteristics of the disease have been fully described by Bartholomew and co-workers, who have found that, during rapid transpiration (in arid or semi-arid conditions, regardless of the amount of water in the soil, the roots and conducting tissues of the shoot are not able to deliver water to the leaves as fast as it is needed. Under such circumstances water is withdrawn from the fruits. This fact may account (at least in part) for the deterioration, which is known as *internal decline*.[1]

Citrus aurantifolia Swingle (=*Limonia aurantifolia* Christmann, = *C. limetta* of some authors, but not of Risso) is the sweet lime of India, where it is said to be indigenous in the Nilgiri hills. It is a small tree, and more sensitive to cold than any other species or variety of the genus. A few warm days in winter cause it to put forth fresh growth which is killed with the return of freezing weather. It is widely cultivated in warm regions, its cultivation in Florida being largely confined to the Keys. The

[1] Bartholomew, *et al.* Am. Jour. Bot. **13**: 102–117. Feb., 1926; *Ibid.* **10**: 67–70. Feb., 1923.

ripe fruit is greenish yellow, the thin peel noticeably dotted with glands, and the greenish pulp has a very acid juice which is used to make limeade, more highly esteemed by some than lemonade. Bottled lime juice is an article of commerce, and is used in the making of lime drops. Pickled limes are also popular with many.

MAHOGANY FAMILY

The Mahogany Family (*Meliaceae*) is composed mostly of tropical or subtropical trees, shrubs, or shrubby herbs, in several of which the wood is odorous. The alternate leaves, without stipules, have pinnately compound blades—sometimes thrice pinnate. The leaflets may be entire or toothed. The perfect or polygamo-dioecious flowers are borne in a panicle. There are 3–5 sepals and 3–5 petals, the latter distinct or somewhat united. There are 8–10 stamens and 3–5 united carpels. The family takes its name from the genus *Melia*, one species of which (*M. Azedarach*), is a large ornamental tree, the Pride-of-India or China-tree, naturalized in the southeastern United States from Asia. Among the important genera, commercially, are the following.

Mahogany (*Swietenia Mahogani*), a very large evergreen forest tree, 75 or more feet high, with a trunk 10–12 feet in diameter, swollen at the base. The heavy wood, as is well known, is highly prized for furniture and cabinet work, and is extensively used as a veneer over a less expensive and lighter weight wood.

West Indian Cedar (*Cedrela odorata*), a subtropical tree which greatly resembles its relative, the Ailanthus or Tree-of-Heaven, furnishes the fragrant wood of which cigar boxes and other objects are made. Another species of this genus, *Cedrela sinensis*, is hardy as far north as Long Island, and is a very beautiful ornamental tree. *Cedrela Toona* is an important timber tree of India, and the lumber derived from it is often called Indian Mahogany.

The remaining families of the Geraniales—Wood-sorrel Family (*Oxalidaceae*), Ailanthus Family (*Simarubaceae*), Milkwort Family (*Polygalaceae*), and others, have only slight economic importance, and contain few, if any, crop plants.

ORDER, Sapindales

Among the families of this order containing species of economic importance are the following:

Box Family (*Buxaceae*), named from *Buxus*, the Box or boxwood, one of the most satisfactory shrubs for clipped hedges and topiary work.

FIG. 448.—Mango tree (*Mangifera indica*) in fruit.

Cashew Family (*Anacardiaceae*), containing the sumachs—*Rhus typhina* (Staghorn Sumach), *R. Vernix* (Poison Sumach)

R. Taxicodendron (Poison Ivy), *R. quercifolia* (Poison Oak), and others. Here, also, belongs the Mango (*Mangifera indica* (Fig. 448). The Cashew nut, of commerce, is the kidney-shaped fruit of *Anacardium occidentale*, borne on a greatly enlarged receptacle, resembling a seed on the outside of a ripened ovary (Fig. 449).

Holly Family (*Aquifoliaceae*), containing the following broad-leaved evergreen shrubs, much used for decorative planting:

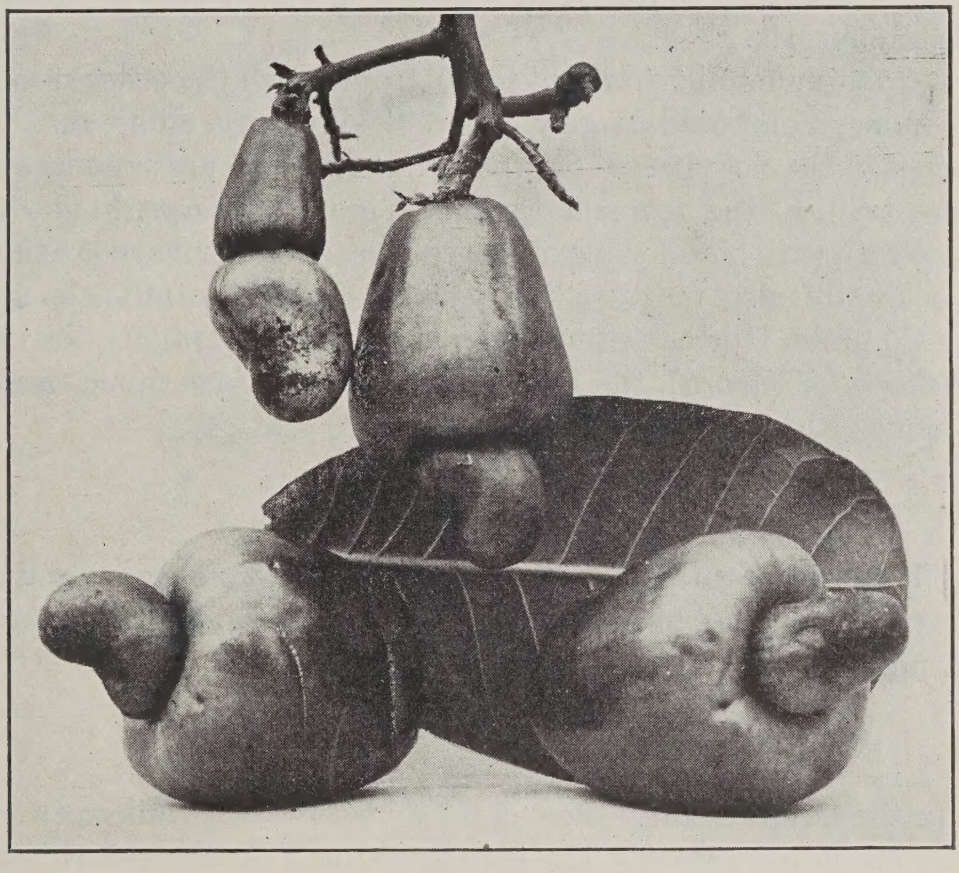


Fig. 449.—Fruit and leaf of Cashew nut (*Anacardium occidentale*).

American Holly (*Ilex opaca*), English Holly (*I. Aquifolium*), both extensively used for Christmas decorations; Inkberry (*I. glabra*), *Ilex crenata*, and others. The Black Alder (*I. verticillata*) is not evergreen.

Staff-Tree Family (*Celastraceae*), including the Burning Bush or Waahoo (*Euonymous atropurpureus*), and the Climbing Bittersweet (*Celastrus scandens*).

Maple Family (*Aceraceae*), including the various species of Maple (*Acer*). The sugar maple (*Acer saccharum*) gives an

abundance of sap which is collected in early spring by "tapping" the trees. After boring a hole through the bark and into the wood, a metal or wooden spigot is inserted, through which the sap flows out and is caught in a pail or bucket. A warm day following freezing temperatures the preceding night favors the flow of sap. The sap is then evaporated or "boiled down" to make maple syrup. By further boiling, maple sugar is made. It is said that the process of making maple syrup and sugar was taught to the white settlers by the Indians in Western Massachusetts.

Soapberry Family (*Sapindaceae*), from which the order receives its name, composed largely of tropical woody climbers. The berries of the Soapberry (*Sapindus Drummondi*) are saponaceous. Here belongs the tropical Balloon Vine (*Cardiospermum Halicacabum*), with bladder-like pods, cultivated in northern latitudes. The family also includes the various Horsechestnuts, such as the Common Horsechestnut (*Aesculus Hippocastanum*), the Ohio Buckeye (A. *glabra*), the Red Buckeye (*A. Pavia*), much used as ornamental trees, and other species.

ORDER, Rhamnales

This order, containing the Buckthorns (*Rhamnaceae*) and the Grapes (*Vitaceae*), has a single whorl of stamens inserted opposite the petals.

Grape Family

In the Grape Family the 4–5 petals very readily fall away soon after the flower opens. The plants are vines (as the generic name indicates), climbing by tendrils which are modified branches. The fruit is a berry, usually with two cells and four seeds. There are some 20–25 species of wild grape in the United States. The genus is also found wild in Africa, southern Europe, and western Asia. De Candolle suggests that, on account of its dissemination by birds, it must have had a wide geographical distribution even before the existence of man in Europe or even in Asia. This is one of the most anciently cultivated of all known plants. Seeds found in the lake dwellings near Parma (northern Italy), and other evidence, carry the date of its cultivation back to the prehistoric

age of bronze. There are records of its cultivation in Egypt at least 6000 years ago.

It seems probable that wine was made by prehistoric man from the uncultivated *Vitis vinifera*—the "wine-bearing *Vitis*," which is the grape of ancient and modern European cultivation (Fig.

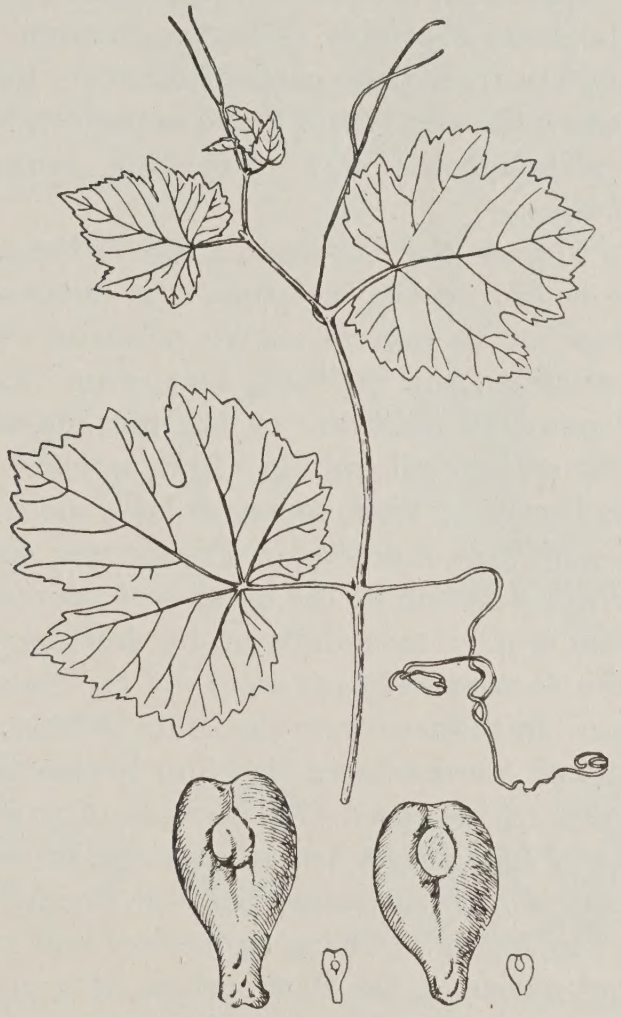


FIG. 450.—European grape (*Vitis vinifera*). Twig with leaves and tendrils, ½ natural size (after Dippel); seeds, natural size and enlarged (after Engelmann). (From Bessey, C. E. Nebraska Hort. Soc. Ann. Rept. 1895.)

450). Its probable habitat is the region around the Caspian Sea, whence it has spread, by Phoenician commerce and otherwise, throughout Europe, Asia, and Africa. The European grape differs from the American species in having a higher sugar content and more solid matter in the fruit—qualities which render it specially valuable for the making of wine and raisins. The

American grapes, lacking these qualities, are most valuable for table use.

In 1616 Lord Delaware introduced the culture of the Old World grape into the New World, but without success. Then in 1719 the Colonial Assembly of Virginia passed a law compelling every householder to plant and cultivate at least ten cuttings. Twenty years later the same Assembly offered a premium for successful grape growing, but from these early attempts to the present time all efforts to grow the Old World grape in eastern North America have failed—although it is now successfully grown west of the Rocky Mountains.

The failure to grow the European grape in the eastern United States is due chiefly to the fact that it is not resistant, as the American grape is, to several native parasites—the root-louse (*Phylloxera vestatrix*), and the fungi that cause black-rot, downy mildew, and powdery mildew. In the northeastern states the climate is unfavorable, but even in Virginia, where the climate is congenial, the European vines sooner or later succumb to disease.

The grape and wine industry of France was some years ago threatened with extinction by the ravages of the root-louse. The vineyards were finally reestablished by grafting the European varieties on Phylloxera-resistant stocks of the New World grape (*Vitis Labrusca*), introduced from the United States.

Experiments of Averna-Saccà[1] led him to conclude that resistance to Phylloxera increases with increase of natural acidity of the vines; it was found that American vines, grown in southern Italy, and especially if on calcareous soil, tended to lose their resistance to Phylloxera. Owing to the fact that Phylloxera and mildew are not native on the Pacific slope, it is possible to grow the European grape there with entire success. In fact, the California climate is so favorable that *Vitis vinifera* tends to run wild.

The principal cultivated varieties of American grapes, especially in the north, were derived from *Vitis Labrusca* (Fig. 451), often called the "fox grape," possibly because of its odor, which resembles that of the fox. The southern domesticated forms were

[1] Averna-Saccà, R. The acidity of the sap of American vines in relation to their resistance to phylloxera, according to Comes. Abstract in Exp. Sta. Record **25**: 463. 1911.

probably derived from the Muscadine (*Vitis rotundifolia*). (Fig. 452). A few varieties (*e.g.*, Agawam and Lindley) are hybrids between *V. Labrusca* and *V. vinifera*.

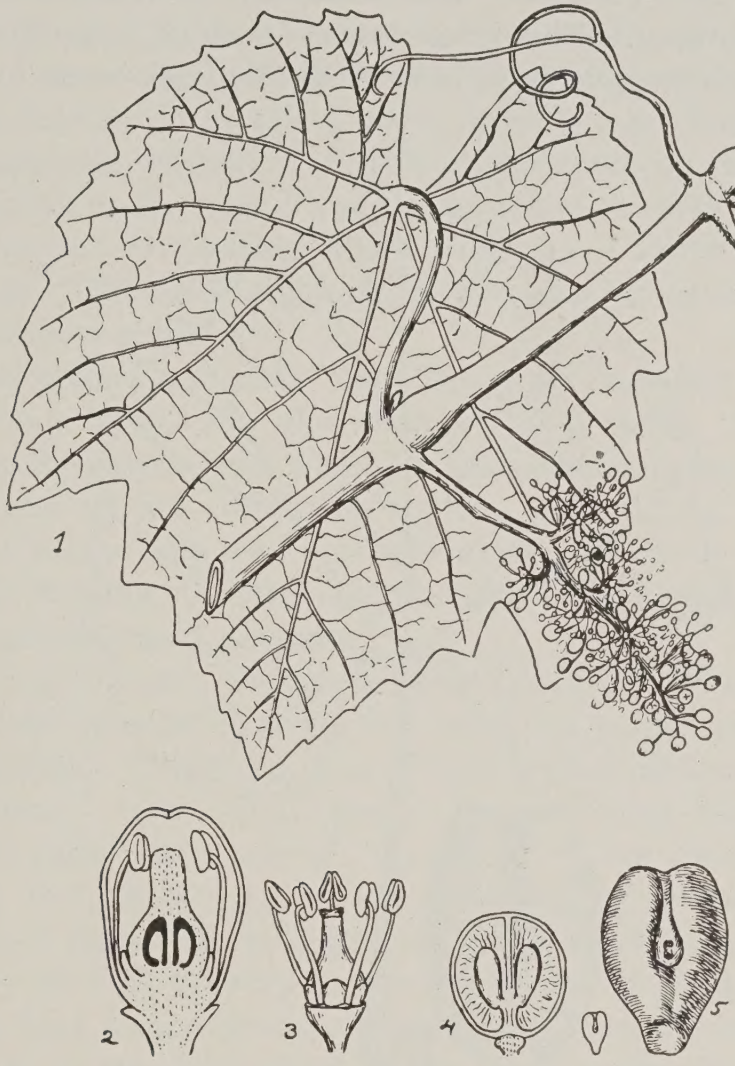


FIG. 451.—Northern Fox Grape (*Vitis Labrusca*). 1, portion of twig, with leaf, inflorescence, and tendril, about natural size; 2, median longitudinal section of a perfect flower, enlarged; 3, perfect flower (enlarged), with petals removed; 4, longitudinal section of fruit (berry); 5, seeds, natural size and enlarged. (1–4 after Gray; 5 after Engelmann, from C. E. Bessey. Nebraska Hort. Soc. Ann. Rept. 1895.)

The Concord grape is the best known of all American varieties. Its botanical characters, as Hedrick[1] and others have noted, indicate that it is a pure bred *Labrusca*. The first Concord grape-

[1] Hedrick, U. P. The grapes of New York. N. Y. State Dept. Agr. 15th Ann. Rept. Vol. 3, Part II. Albany, 1908.

vine was produced by a seed of a wild *Vitis Labrusca*, planted at Concord, Massachusetts in the fall of 1843 by Ephraim W. Bull (Fig. 685). It first bore fruit in 1849, and was exhibited for the first time in 1852 before the Massachusetts Horticultural Society.

Seedless Grapes.—The grape ovary normally contains four ovules, but only rarely do all of these develop into seeds. Berries

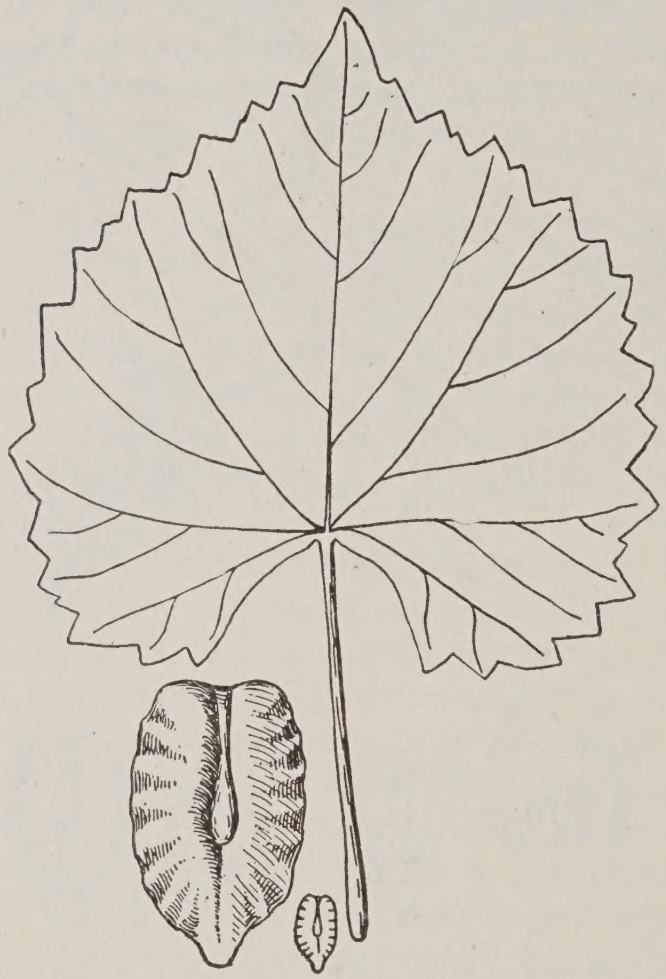


FIG. 452.—Muscadine or Southern Fox Grape (*Vitis rotundifolia*). Leaf, ⅔ natural size (after Dippel); seeds natural size and enlarged (After Engelmann.) (From C. E. Bessey, Nebraska Hort. Soc. Ann. Rept. 1895.)

with one or two seeds are most common, and then, in order, seedless berries and berries with three and four seeds.[1] The formation of seeds is, of course, dependent upon the fertilization of the ovules, and since pollination varies greatly with the

[1] Müller-Thurgau, H. Dependence of the fruit development of grapes and some other fruits on the development of the seed. *Landw. Jahrb.* Schweiz. **12**: 135–205, 1898. Abstract in Exp. Station Rec. **11**: 932–936.

weather, the seediness of the grapes is, in normal varieties and within certain limits, also a function of the weather, and therefore varies from year to year. The size of the grape increases greatly with the number of perfect seeds it contains, the process of fertilization and seed development apparently stimulating the growth of the ovary. The fewer the number of seeds the earlier the fruit ripens, the ripening being earliest in seedless varieties.

In grapes, the formation of fruit is dependent on the germination of pollen on the stigma and the growth of the pollen-tube into the ovary; but fertilization of the ovules is not necessary to fruit formation. Müller-Thurgau gives three conditions necessary to secure seedless grapes:

1. The pollen-tube may enter the ovary, but fail to fertilize the ovules. In this case the seedless fruit is small. This is the case with the grapes from which Corinthian raisins are made, and with several other European varieties.

2. The pollen-tube may enter the ovule, but the ovule may be incapable of being fertilized. In this case the ovules may develop slightly and the fruit is larger.

3. The pollen may be defective, although the ovules may be perfect and capable of being fertilized. If pollen germination fails completely the flowers drop off and no fruit is formed.

"*Currants.*"—The small dried fruit resembling small raisins, and sold under the name of "currants," is not obtained from currants (*i.e., Ribes*) at all, as most people doubtless infer, but from a variety of the European grape, *Vitis vinifera*. Pliny mentions them as growing in Greece in 75 A.D., and they were probably first imported into Europe from Corinth, for they are referred to in the old herbals of the 14th to the 16th centuries as "reysyns de corauntz," "raysns of Coren," "currans," and finally *currants*.[1] The growing of these currants has been one of the principal industries of Greece. This species has undoubtedly been propagated by cuttings for many centuries.

Hothouse Culture.—Only the European grape (*Vitis vinifera*) is grown under glass. To insure the enormous bunches of large grapes severe pruning is resorted to, with a view to the storing

[1] It seems probable that the name "currant" was applied to certain species of the genus *Ribes* because of the resemblance of their fruit clusters (racemes) to those of the "grape of Corinth."

up of nutrient material in a few lateral buds, which, in turn, are thinned to a foot or more apart, so that the vine grows only about one pound of fruit to a foot of main stem.

The Virginia Creeper (variously known by the generic names, *Ampelopsis*, *Parthenocissus*, and *Psedera*), and some 9 other genera and 450 species are included in the Vitaceae.

CHAPTER XXXI

POLYPETALOUS DICOTYLEDONS (CONTINUED)

ORDER, Malvales

In the order, *Malvales*, belong the species of Basswood or Linden (*Tilia*), the Mallows (*Malvaceae*), including the Marshmallow (*Althaea*), Musk Mallow (*Malva moschata*), Indian Mallow (*Abutilon*—a common weed of plowed fields), Rose Mallow (*Hibiscus*), Okra (*Hibiscus esculentus*), the Cotton

FIG. 453.—Linden (*Tilia Michauxii*), Branch with leaves and flowers.

plant (*Gossypium*), and others. Most of the species in the order have abundant mucilage and the surface thickly covered with hairs. The usually numerous stamens are either united in groups or are monadelphous.

The *Linden Family* (*Tiliaceae*) includes the American Linden or Basswood (*Tilia americana*), Bee-tree (*Tilia heterophylla*), the European Lindens and the important fiber-producing plant, Jute (*Corchorus*) an Old World genus cultivated in the tropics. The genus *Linden* has an added interest for the botanist, for its Swedish name, Lind, was the origin of the family

name of the father of modern systematic botany, Linneaus.[1] The cream-colored flowers are in cymes, and the peduncle is united to a tongue-shaped, membranous bract (Fig. 453).

Fig. 454.—Chocolate tree (*Theobroma cacao*). (Philippine Bureau of Science.)

STERCULIA FAMILY

The Sterculia Family (*Sterculiaceae*) resembles the *Malvaceae* in having its stamens frequently monadelphous, and in the char-

[1] The paternal grandfather of Linnaeus was a Swedish peasant, named Ingemar Bengtson. Two of his brothers, great uncles of Linnaeus, became university graduates and clergymen, and following a social custom, current in their day, they changed their family name, choosing the Greek name *Tiliander*, in allusion to a stately linden or *Tilia* that grew near their home. The name means, then, Lind-tree-man, or in Swedish, Lindman. The father of Linnaeus, Nils Ingemarson (*i.e.*, Ingemar Bengtson's son) also became a learned clergyman and chose the Latin form of Lindman, namely *Linnaeus*. In 1761 Carl was granted a patent of nobility to date from 1757, and thereafter he became known (in Swedish) as Carl von Linné.

acter of its foliage. There are over 600 species, all tropical or sub-tropical, distributed in over 50 genera. The genera are classed in 8 tribes.

The genus *Sterculia*, comprises some 90 species, most of which are large trees. The inner bark of some of them yields a tough fiber used for paper, mats, and cordage. The mucilaginous seeds of some species yield an oil used in lamps, and a gum similar to gum tragacanth.

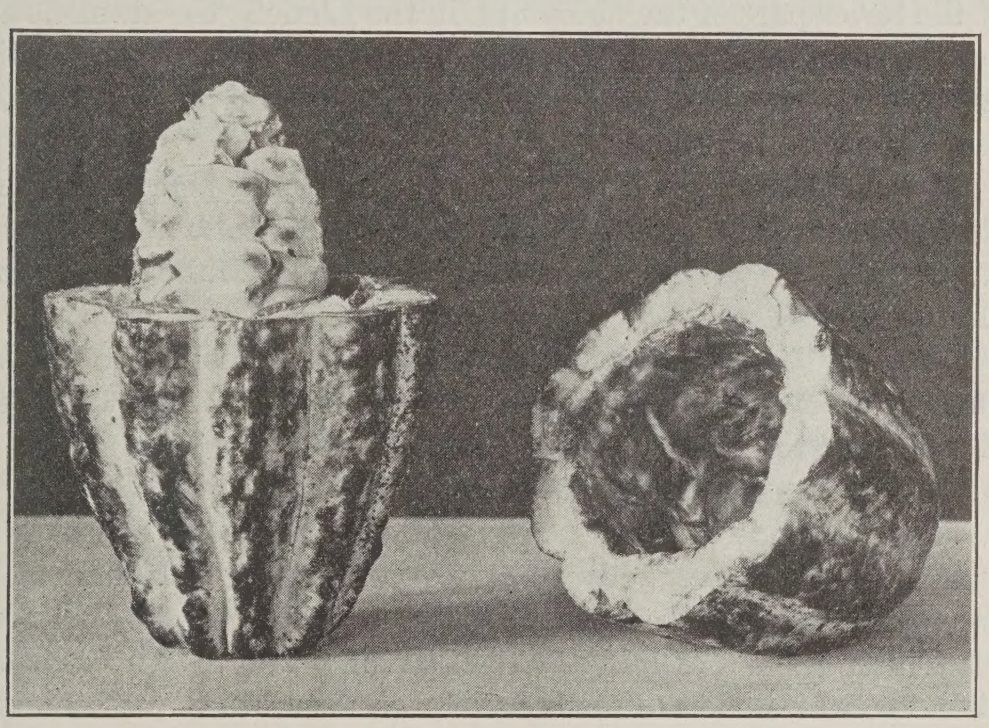


FIG. 455.—*Theobroma cacao.* Fruit, dissected so as to show the seeds which are the source of chocolate.

The Cola tree (*Cola acuminata*), native of tropical Africa, is the source of the Cola nuts of commerce. They are, in reality, seeds which contain the alkaloids, thein (found also in tea and coffee) and theobromine (found also in chocolate).

One of the most important species, commercially, is the Chocolate tree, *Theobroma cacao* (Fig. 454), a moisture-loving, small tree native in Central and South America, but now cultivated generally in tropical countries of both hemispheres. The oily seeds (Fig. 455) are the source of oil or butter. A cheaper butter, prepared from the oil of the coconut, is sometimes called "cocoa butter," a name easily confused with "cacao butter."

The most important product of *Theobroma cacao* is the chocolate of commerce. This is prepared by grinding the roasted seeds and flavoring the resulting paste with sugar, vanilla, or other flavoring materials.

MALLOW FAMILY

The Mallow Family (Malvaceae) differs from the Tiliaceae in having monadelphous stamens united in a column by the fusion of the lower part of the filaments; in the Lindens the stamens are usually united in several groups (*polyadelphous*). The families are also otherwise distinct. By some, the family is divided into two Tribes, as follows:

Tribe I. Malveae, with the column of stamens bearing anthers clear to the top. Here belong the Indian Mallow (*Abutilon*), Marsh Mallow (*Althaea*), Common and Musk Mallows (*Malva*), and other genera.

Tribe II. Hibisceae, with the column of stamens not bearing anthers clear to the top, but naked and 5-toothed at the apex. Here belong the Rose Mallow (Hibiscus), and other genera.

The most important plants of the Order are in this Family.

The fruit pods of *Hibiscus esculentus* are the source of *okra* or *gumbo*, used to give body to catsup and soups. The mucilaginous pods are prized by some as a stew, and they may be preserved for winter use by canning or dissication. The brown or black, globular, white-spotted seeds have been used, when roasted, as a substitute for, or adulterant of, coffee. Okra grows as a perennial when protected from frost. The pods must be gathered before they become fibrous. In the southern United States there are dwarf varieties which fruit earlier than the type. This is a very old culinary plant, known to the Spanish Moors, and in common use in Egypt as early as 1216 A.D.[1] Its cultivation reached Brazil before 1648, and it was in general cultivation in the United States in the first decade of the nineteenth century. It is interesting to note that the Italian name for okra is *ibisco*.

COTTON

The most important species of Malvaceae cultivated as a crop is cotton (Arabic, *Qutn*). This plant was found under cultivation

[1] Sturtevant, E. L. The history of garden vegetables. Amer. Nat. **24**: 30, 143, 313, 629, 719. 1890.

in America when the continent was discovered by the Spaniards, and cotton growing is now the chief industry of eight or ten of the United States, comprising about one fourth of the total area of the country. In fact cotton has been called the most valuable "money crop" of the Union, the value of the annual crop being exceeded only by corn, which is grown in every state, and by wheat, also grown on a larger area. As a former assistant secretary of agriculture[1] has pointed out, "its economic importance is far beyond numerical expression; for while the total crop of the world is approximately ascertainable, the effect of cotton upon the commercial and social relations of mankind is too far reaching for estimation."

While cotton is said to drain the fertility of the soil less than any other crop, it yields a number of commercial products of great value and indispensable to modern society. These products include the fibers on the seed, known as lint, cotton-wool, or merely as "cotton;" cotton-seed oil; cotton-seed meal, used as feed for stock; a fiber from the stems; and a drug from the roots. The lint is used not only for the manufacture of cotton cloth, but also in the manufacture of *guncotton*, which is made by soaking clean, dry cottonlint in a mixture of strong nitric and sulphuric acids. The sulphuric acid and sulphur compounds are eventually removed by thorough washing, leaving a nitrate of cellulose, or possibly a mixture of nitrates, highly explosive, and to which the name guncotton is applied. Its use in guns is possible only after it has been gelatinized or transformed into the colloidal state by chemical treatment.

Cotton-seed meal is very rich in nitrogen and is therefore valuable as a fertilizer, since nitrogen is the most costly as well as the most essential ingredient of fertilizers (*Cf.* p. 222). Cotton-seed oil is injurious to plants, and hence the seed-meal becomes valuable as a fertilizer only after the oil is thoroughly removed.

Since the nitrogen in cotton seeds is in the form of protein, the meal is even more valuable for feed than for fertilizer. Thus, by the application of scientific knowledge and methods, the cotton seed, which was once a troublesome problem or nuisance, involv-

[1] Dabney, Chas. W. The cotton plant. U. S. Dept. Agr. Office of Experiment Stations. Bull. No. 33. Washington, 1896.

ing expense but not profit, has become second only to the lint as a commercial product of the cotton plant.

The Hindoos appear to have been the first to weave cloth out of cotton fiber, and for upwards of 3000 years (1500 B.C.–1500 A.D.) India was the center of the cotton industry. Herodotus and other early writers refer to "trees" in India, "the fruit of which is a wool exceeding in beauty and goodness that of the sheep;" and the same author refers to the soldiers in the army of Xerxes as wearing cotton clothing. Pizarro found cotton in

FIG. 456.—Cotton field in Louisiana. (After C. W. Edgerton, Louisiana State Agr. Exp. Sta.)

use in Peru in 1522, and it was in general use in the new world between latitudes 40° north and 40° south (except in the present "cotton belt" of the United States) when America was first settled.

In 1775 the legislatures of South Carolina and of Virginia recommended the cultivation of cotton; in 1786 Thomas Jefferson referred to its growth in the Southern States, and James Madison expressed his belief that "the United States would one day become a great cotton-producing country." It was in the latter year that Sea-Island cotton was introduced into Georgia from

the Bahama Islands. The invention of the cotton gin by Eli Whitney, about 1793, did more than any other one thing to increase production, the amount of cotton exported from the United States increasing from 487,000 pounds in 1793 to 1,600,000 pounds in 1794—the year that Whitney's gin was patented.

Botanical Characters.—There are several species of the genus *Gossypium*, all of more or less economic importance, such as *G. arboreum*, *G. neglectum*, *G. brasiliense*, *G. herbaceum*, *G. barbadense*, and others. Only the herbaceous cottons are cultivated to any great extent in the United States (Fig. 456), and there appears to be some difference of opinion among systematists as to just what species are represented by the 50 or more varieties of Upland, Sea Island, and other forms. Wild cotton is an arborescent, shrubby, or herbaceous perennial, but the cultivated herbaceous forms are either annual or biennial. The plants are usually hairy throughout, and all parts of the stem, flower, leaves, fruit, and sometimes the cotyledons, have numerous small glands, that look like black spots on the surface (Fig. 457).

Leaf Arrangement.—The leaves (and therefore the branches) on the main stalk and on the branches are in spirals, and the leaf arrangement (*phyllotaxy*) of the new world species differs from that of the old world species. In the New World or Upland and Sea Island species (*e.g.*, *G. hirsutum*, *G. barbadense*), and the closely related native forms of tropical America, the leaves are arranged in three-eighths spirals; that is, if one starts with a given leaf on the lower part of the stem and passes to each upper leaf in succession he will pass eight leaves on an upward spiral of three turns before coming to a leaf (the ninth one) located directly above the leaf with which he started. The arrangement may be made clearer by connecting the bases of the leaves with a white thread.

In the Old World species and varieties (*G. herbaceum*, *G. arboreum*, and others) the leaves have a one-third arrangement; that is, in starting from a lower leaf one will pass two leaves on a spiral of one turn before coming to a third leaf which is directly above the leaf with which one started. The spirals vary from left-handed to right-handed, apparently without rule.

Leaf Movements.—Cotton leaves have, at the base of the petiole and at the base of the lobed leaf-blade, a motile organ or *pulvinus*. By means of these organs the leaves are kept constantly adjusted

to the direction of the sun's rays. The basal pulvinus moves the entire leaf, while the distal one moves the leaf-blade independently. According to Meade[1] the leaf-blades face east in the morning and west in the afternoon. At night the leaves droop, like those of many legumes, although they are more turgid then than during the day.

Roots.—The Cotton plant has a tap-root with lateral branches which may grow vertically downward in the soil after having grown obliquely for some distance. King, who was the first to record this observation, states further that there is no appreciable difference in the size or distribution between the roots of large plants and those of small plants. Most of the tap-roots, he says, of both large and small plants were found (in the plants studied by him in Arizona) to extend to a greater depth than 7 feet, and the only one followed to its greatest depth measured 10 feet, 8 inches in length. A considerable number of secondary roots extended to great depths and apparently shared the function of the tap-root. The root-system, therefore, becomes a limiting factor in the absorption of water from the soil, and a large plant with many leaves may lose water by transpiration faster than it can be supplied by the root system. The soil about the roots may, in other words, have its available water exhausted faster than it can be renewed by capillary action from more distant soil. The result is what is called "water-stress" in the plant.

Branches.—There are two kinds of branches, vegetative and fruiting. The fruiting branches are developed from *extra-axillary* buds formed at the side of the axillary buds.[2] Fruiting branches are borne on the upper portion of the main stem; the lower branches of the main stem are vegetative, and they, in turn, may also bear fruiting branches. Change of environment may cause either kind of branch to transform into the other. The flower-buds (called *squares* by the growers) are borne on the fruiting branches—one to each joint; they have been considered homolo-

[1] Meade, R. M. Positions and movements of cotton leaves. Jour. Heredity. **12**: 444–448. Dec., 1921.

[2] Cook, O. F., and Rowland M. Meade. Arrangement of parts in the cotton plant. U. S. Dept. of Agr. Bur. Plant Industry. Bull. No. 222. Washington, 1911.

gous to the extra-axillary buds from which the fruiting branches arise. The flower is surrounded by an involucre of three (rarely two or four) leafy bracts or bracteoles (Fig. 457). Some species, (*e.g., G. vitifolium, G. punctatum*) have stipular bractlets. The calyx has five lobes, usually quite small and often with super-

FIG. 457.—Flower of Cotton, with one petal removed. Note the glands (black dots) on the calyx. (After C. W. Edgerton. Louisiana State Agr. Exp. Sta.)

numerary lobes. Cook regards the calyx as an inner involucre. The common function of the calyx, namely, the protection of the young flower-bud, is, in cotton, performed by the large bracts of the involucre. The stamens, frequently branched, are in five vertical rows. The petals are opposite the lobes of the staminal column. In Sea Island and Egyptian cottons the petals

have a prominent red spot near the base; this spot is absent from most varieties of upland cotton. It has been observed, in Pima cotton, that the spot is not so well developed in small flowers on stunted plants as in the larger flowers on vigorous plants. There is also considerable variation in the spots among the flowers of an individual plant.[1] The number of carpels (which is the same as the number of stigmas) varies, being 2–4 in Egyptian cotton, 3 in Sea Island, and 3–5 in Upland. The fruit (*cotton-boll*) is an oval, pointed capsule of a shining green color, 3–5 valved, and as long as or longer than the persistent involucre. In each cell of the capsule there develop either one seed, as in the woody, imperfectly dehiscent fruit of *G. drynarioides*, or seven to nine seeds, as in some of the more highly developed cultivated species. Each seed of the cultivated varieties is covered with the silky fibres (the *staple*), which form the "cotton-wool," "floss," or "cotton" of commerce. The floss of wild and uncultivated species of *Gossypium* is prevailingly rust-colored, reddish, or yellowish, but in the cultivated strains the color has been bred out, and the wool is white.

Watt[2] considers the fleece characters as of great systematic value, and on this basis divides the species of *Gossypium* into five sections as follows:

Section 1. *Species with a fuzz but no floss*, including *G. tomentosum* and several other species. No cultivated forms are known of this species.

Section II. *Seeds with both fuzz and adherent floss, and with bracteoles united*, including *arboreum, Nanking, obtusifolium, herbaceum*, and their varieties. *G. herbaceum* is one of the most, if not the most, important of the annual cottons.

Section III. *Seeds with fuzz and adherent floss: bracteoles not* united, including *hirsutum* and eight or nine other species.

Section IV. *Seeds naked (i.e., no fuzz), and floss easily removed. Bracteoles free or nearly so, and glands conspicuous.* Includes some five species. Here belongs the Sea Island Cotton (*G. barbadense* var. *maritima*), cultivated most successfully on Islands off the

[1] Kearney, Thomas H. Inheritance of petal spot in Pima Cotton. Jour. Agr. Res. **27**: 491–512. 1924.

[2] Watt, Sir George. The wild and cultivated cotton plants of the world. London, 1907. Watt also considers the glandular characters of value in classification.

coast of the Carolinas and Georgia. It is said that the Sea Island cotton, when first introduced into America, was perennial (like *G. barbadense*), and that the prevailing annual type was produced by selecting seed from plants that matured their pods before the mild winter set in.[1] The presence of two kinds of pollen grains, together with other characters and their behavior, indicates that Sea Island cotton is probably of hybrid origin. The pollen resembles that of the two forms that have been regarded on other grounds as the probable ancestors.

Section V. *Seed naked, bracteoles quite free, glands absent.* Includes only one species, viz. *G. Kirkii*. Not known under cultivation.

Mercerising.—In 1850 John Mercer discovered that if cotton fibre is soaked for about an hour in a concentrated (33%) solution of caustic soda it becomes stronger and finer, and can be dyed to better advantage. This treatment is called mercerising.

Diseases of Cotton.—Like most crop-plants, the cotton plant is subject to numerous diseases, some (such as the yellow and red leaf-blights, shedding of bolls, etc.) are probably due to *physiological causes*, some (such as seedling-rot, root-rot, cotton-boll-rot, etc.) are due to *bacterial causes*, one (the root-gall) is caused by a parasitic nematode worm (*Heterodera radicicola*), and others (such as the cotton worm, the cotton-boll worm, and the cotton-boll weevil) are due to *insects*.

The *cotton worm* (or cotton caterpillar) is active all summer in the cotton fields of the southern United States, feeding on both surfaces of the leaf. It is not a worm, but the larva of a moth (*Aletia argillacea*).

The *cotton-boll* worm is the larva of the moth (*Heliothis armiger*), and attacks corn and tomatoes as well as cotton. In fact, the cotton-boll worm, corn-ear worm, and tomato-fruit worm are all the same species,[2] which also ravages several other

[1] "In the days of slavery the individual estates under cotton were large—say 400 to 500 acres—now they are rarely more than 50 to 60 acres. In the former system the yield did not exceed 80 to 100 lbs. to the acre, now 250 to 400 lbs., or even close to 600 lbs. of ginned cotton, is the usual outturn." Watt, *l.c.*, p. 283.

[2] Howard, L. O. The insects which affect the cotton plant in the United States. U. S. Dept. Agr. Office of Exp. Sta. Bul. No. 33, pp. 317–350. Washington, 1896.

crops, such as legumes, cucurbits, tobacco, and numerous flowering plants, such as geranium, gladiolus, and others.

The *Mexican cotton-boll weevil* (Figs. 458 and 459), one of the chief insect enemies of the cotton plant, is the larva of a beetle (*Anthonomus grandis*). This insect has several times destroyed the entire cotton crop in certain sections of Mexico, even causing the temporary abandonment of the attempt to raise cotton. It crossed the Rio Grande in 1893, near Brownsville, Texas, and has since spread throughout the cotton region of the United States, having advanced northward at an average rate of about 50 miles per year. The weevils advance normally by the flight of the adult insects, but they may rapidly be carried long distances when caught in strong wind currents at a high elevation. This probably explains the greatest advance of the weevil ever known in any one year, in 1915. Between August 20 and 23 of that year the weevils advanced in a general northeasterly direction across Alabama to a line over 140 miles from the northern limit of the preceding year. The explanation is found in the high south and southwest winds following the famous Galveston hurricane of that year.[1]

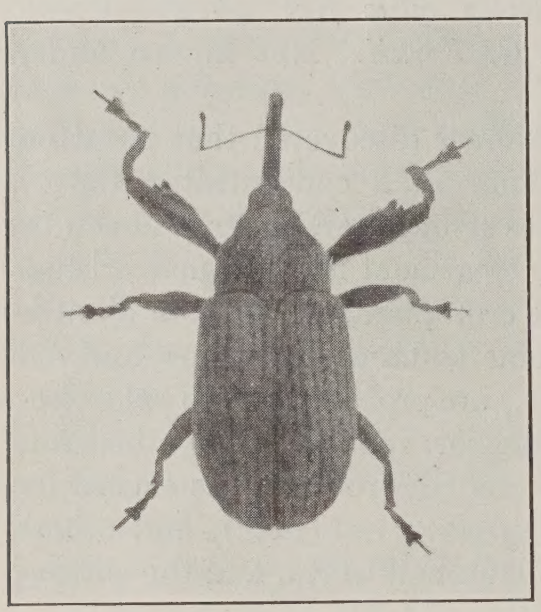


FIG. 458.—Cotton-boll weevil (*Anthonomus grandis*). Imago. (From U. S. Dept. Agr. Bur. Entomology, through B. R. Card, Delta Laboratory, Tollulah, Louisiana.)

Control measures include the following: (1) Fall burning of cotton stalks which afford the best shelter for the hibernating adult (*imago*); (2) Raising only as much acreage as can be given proper attention in control measures; (3) Early planting; (4) Picking the weevils when squares begin to form, and destroying infested squares. (5) Prompt picking in the fall. Early fall destruction of the stalks is considered the most important meas-

[1] Hinds, W. E. Boll weevil in Alabama. Alabama Agr. Exp. Sta. Bul. 188. 1916.

ure of all, since it prevents late fall breeding. Treating plants with insecticides has not proved very effective.

There are about 30 kinds of insects which feed upon the weevil at some stage of its life-history, chief of which is the "fire ant;" there are 25 or more parasites that live on it as a host, and some 50 or more birds that feed on it. Doubtless the most successful

FIG. 459.—Adult cotton-boll weevils working on a boll. (From U. S. Dept. Agr. Bur. Entomology, through B. R. Card, Delta Laboratory, Tallulah, Louisiana.)

method of all will be the breeding, if possible, of strains of cotton resistant to weevil.

Boll-shedding.—The falling off of some or all of the flower buds and young fruits of plants is a common phenomenon, and in cultivated plants it may often cause a considerable loss of crop. In a plant like cotton, where the commercial product is in the fruit, this early falling off, sometimes of more than half

of the bolls, becomes a very serious matter. The abscission results from the formation, near the base of the flower or fruit stalk, of an "abscission layer," and the subsequent dissolving or digestion of the middle lamella or layer between the cellulose walls of adjacent cells. Lloyd,[1] who made a study of the environmental factors that favor abscission, states that, in Alabama, afternoon rain may cause a high degree of shedding, since it interferes with pollination, and the buds of unpollinated flowers fall early in many other plants. Another factor is fluctuation in the amount of water in the soil due to alternating rain and drought periods. Balls, who studied the problem in Egypt, says that abscission is caused by asphyxiation of the roots following the rise of the water table (see p. 83) during irrigation. From experiments with Pima cotton in Arizona, King[2] concluded that the shedding of squares and bolls was caused by the fact that the soil could not, by capillary action, supply water to the plant as rapidly as it was absorbed by the roots.

"Running Out" of Cotton Varieties.—A gradual deterioration or "running out" of varieties of American Upland cotton has been noted during the last half century, and O. F. Cook has attributed this, in part, to the replacement of private plantation gins by public gins. In the public gins the seed of poor varieties becomes mixed with seed of better varieties. Thus the next crop is composed of desirable and undesirable plants growing together, and by cross-pollination subsequent crops also suffer. Cook also notes that, contrary to a notion generally prevalent among planters, the crossing of plants in different fields, by insect pollination, is an important cause of deterioration or "running out."

ORDER, Parietales[3]

This group of families is highly varied. They nearly all have separate sepals, numerous stamens and *parietal placentation*, whence the name.

[1] Lloyd, F. E. Environmental changes and their effect upon boll-shedding in cotton. Ann. New York Acad. Sci. **29**: 1–31. 1920.

[2] King, C. J. Water-stress behavior of Pima cotton in Arizona. U. S. Dept. Agr. Bull. 1018. March 15, 1922.

[3] Also called *Hypericales*, or *Violales*.

Besides the Violet Family (Violaceae[1]), the Parietales contain the Passion Flowers (*Passifloraceae*), the St. John's-Worts (troublesome weeds of the *Hypericaceae*), the Rock roses (*Helianthemum*, of the *Cistaceae*) cultivated, like the violet, for their beautiful flowers, the Begonias (*Begoniaceae*), the Tea plant (*Thea sinensis* = *Camellia Thea*, of the Tea Family, *Theaceae* or *Ternstroemiaceae*), the Papaya Family (*Caricaceae*, or *Papayaceae*), and others.

FIG. 460.—Sweet White Violet (*Viola blanda*).

VIOLET FAMILY

Of the violets, there are upwards of 150 species, some 40 of which are native to North America north of Mexico. The Sweet Violet (*Viola odorata*) is important in the trade, being the stock from which the numerous florists' varieties are derived. *Viola cornuta* (the Horned Violet) is a European species having various horticultural forms and used as a bedding plant.

In addition to the showy flowers, which are often sterile, there are also *cleistogamous* flowers, borne on runners or shorter flower stalks. These flowers have no petals, never open, and bear an

[1] *Ternstroemiaceae* (in part) of some authors.

abundance of seeds in capsules which open in three valves, with sufficient force to project the seeds to some distance from the parent plant. Among the species of *Viola* having cleistogamous flowers may be mentioned *V. odorata, V. cucullata, V. blanda* (Fig. 460), and *V. palmata.* In *V. odorata* the pollen germinates within the anthers (which never open), and the pollen tubes have to pass through the anther-walls; this is facilitated by the presence of more easily permeable areas of thin-walled cells.

The Pansy or "Heart's-ease," derived from some wild violet, is one of the oldest of cultivated flowers. It is mentioned in Gerard's *Herbal* in 1587, and the name is from the French *pensée* (thought). It is not certainly known from what wild species it was derived, but it is generally considered to have been descended from *Viola tricolor* ("Johnny-jump-up"), a small perennial introduced into America from Europe and still grown in gardens. In England the commercial stock consists of the large flowered varieties of *V. tricolor* intermixed with forms of the indigenous mountain species, *V. lutea.* Although perennial, pansies are commonly grown as winter or spring annuals.

The structure of the flower of *Viola altaica* (the "garden pansy" of England[1]) may be taken as typical of the genus. This species is a native of the alpine and sub-alpine regions of Siberia, and takes its name from the Altai Mts., where it was first collected. The plant may begin to blossom as early as February, and stray blossoms appear as late as November. This long period of blooming makes it valuable as a garden plant. There is a remarkably rich variety of colors, ranging from white through yellow-violet, purple-red, brown, and black. The flowers, solitary in the leaf-axils of the current year, range in size from two to almost three inches in diameter, with two bracts on the flower-stalk just below the flower.

The flower (Fig. 461) is perfect, bilaterally symmetrical, with the parts in fives. One of the green sepals is smaller than the others and there is a flap projecting back over the spur. The lower and larger petal is spurred; the others are somewhat similar to each other, and the color markings converge toward the entrance to the spur. The five stamens have very short filaments,

[1] Church, A. H. Types of floral mechanism. Oxford, 1908. Part I, p. 108.

and form a tube surrounding the ovary. The anthers have interlocking, marginal hairs, and the orange-yellow *connective* is continued as a triangular flap. From the filaments of the two front stamens, long green lobes project into the spur (Fig. 462).

FIG. 461.—English pansy (*Viola altaica*). *a*, ground plan and *b*, median longitudinal section of the flower; *c*, diagram of flowering shoot; *d*, dehiscing fruit showing seeds; *e*, median longitudinal section of a seed, showing the embryo surrounded by endosperm, and the raphe (above to the right). (After A. H. Church.)

These lobes secrete nectar, which accumulates in the spur. The pistil, composed of three united carpels, contains from 50–80 ovules, arranged on three parietal placentas. The enlarged tip of the style contains a cavity, protected by a projecting lip, and

having a stigmatic surface. The anthers and stigma are so arranged that a visiting bee will be dusted with pollen on a certain part of his body, and when he visits another flower for nectar this

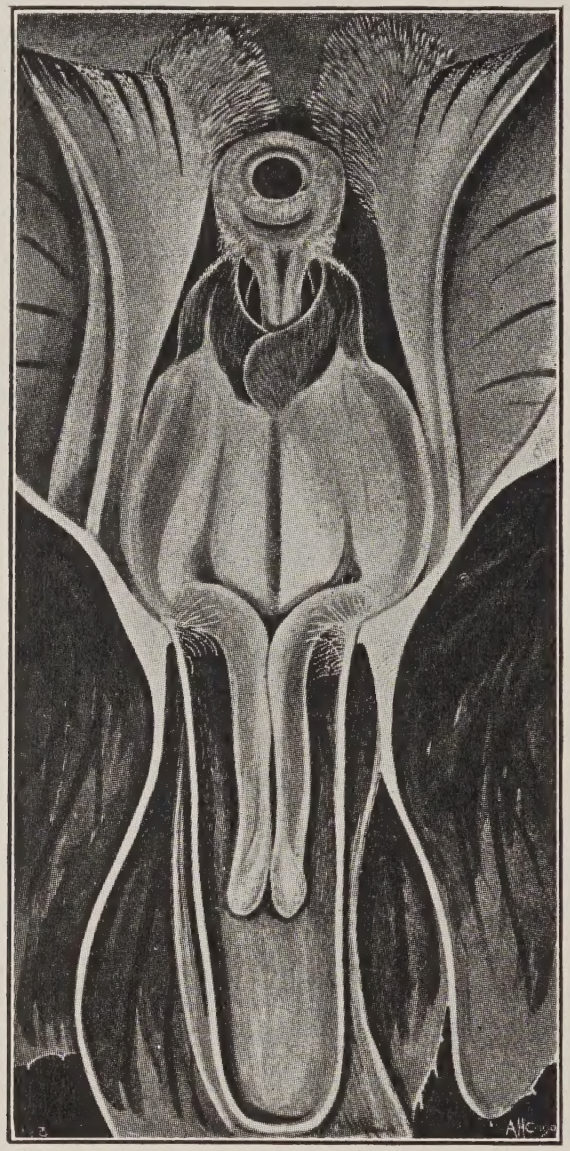


FIG. 462.—*Viola altaica.* General view of floral mechanism from below. (After A. H. Church.)

pollen will be rubbed off into the *germination cavity* of the stigma.

As the fruit matures the three valves open out flat, and by the movement of their margins the seeds are violently ejected, often to a distance of six feet.

CHAPTER XXXII

POLYPETALOUS DICOTYLEDONS (CONCLUDED)

ORDER, Parietales (Concluded)

TEA

By far the most important economic plant of the Parietales is Tea (Fig. 463), of the Tea Family (*Theaceae*). The leaves and young stems, when properly cured and steeped, furnish one of the most generally used drinks of mankind. The flower buds are also used in the highest grade of tea, which has never, until very recently, been exported from China, where it was used chiefly by the aristocracy. The original habitat of wild tea is not known. According to Watt,[1] it was found growing wild or at least escaped from cultivation, in Assam, by Major R. Bruce, about 1824. The development of the industry in India was greatly promoted by Sir Joseph Banks, and later by Colonel Kyd, who was the first to secure seed from China and cultivate it in India (1780). But Watt states that India is largely indebted for the successful development of her tea industry to Lord William Bentinck, who succeeded in acclimatizing the best Chinese plants in India. Watt states that he found the wild tea plant in 1882 growing as a forest tree or large bush in the eastern part of Manipur (India).

The oldest botanical specimen known is in the herbarium of Sir Hans Sloan, the patron of the early English botanist, Ray. The specimen is believed to have been collected in Malabar between 1698 and 1702.

Linnaeus, (in his *Genera Plantarum*, 1737), recognized two genera *Thea* and *Camellia*, which have sometimes been united into one genus, *Camellia*. As the flowers of the tea plant differ in several characters from those of the ornamental camellias,

[1] Watt, Sir George. The commercial products of India. London, 1908. pp. 209–244. The above account is based chiefly upon Watt.

it and the related species are now usually classified in the genus *Thea*, separate from the genus *Camellia*. Commercial tea is the dried leaves of *Thea sinensis*, of which four varieties are

FIG. 463.—Tea (*Thea sinensis*). Flowering branch. One of the five petals has fallen from the flower. Two flower-buds are shown. (From plant in Brooklyn Botanic Garden Conservatories.)

recognized, as follows:[1] *viridis* (having six races and cultivated forms); *bohea* (the chief plant of the black tea countries and

[1] Link accepted two species, *C. Thea* and *C. viridis*.

regarded by planters as a cross between *viridis* and *stricta*); *stricta* (the "Chinese tea" of the Indian tea planters); and *lasiocalyx* (common in Malacca and Panang, and probably a hybrid).

It is not definitely known when the cultivation of tea began, but it was not regularly cultivated in Japan until the 13th century. "That tea drinking in the rest of the world is quite a modern habit may be inferred from there being no classic names either for the plant, the prepared leaves or the beverage, in Japanese, Sanskrit, Arabic, Persian, Hebrew, Greek or Latin." (*Watt*).

Black tea, green tea, and oolong are commercial grades produced by different processes of curing or "manufacture." In making black tea the leaves, after being picked, are allowed to *wither* for about 20 hours at a temperature of 80° F. If the withering is prolonged beyond that time a lower grade of tea usually results. During withering chemical changes take place in the living cells of the leaf, resulting in the formation and accumulation of an enzyme which nearly doubles in quantity during the process.

When the withering is over, the wilted leaf is *rolled* (formerly by hand, now largely by machinery). The purpose of the rolling is to press out some of the juice and bring it into contact with the oxygen of the air. The result of bringing the enzyme into contact with the oxygen is *fermentation* (in this case oxidation). Katayama,[1] a Japanese student, showed experimentally that the aroma of black tea is produced by the action of an enzyme and not by bacterial action.

After fermentation has been allowed to proceed for 2–6 hours it is rapidly stopped by quickly drying the leaves. This is called "*firing*," as it was formerly done by placing the leaves on trays over charcoal fires. The initial temperature is 220°–240° F, and is later reduced by 180°–200° F. If the firing is *not* done quickly the tea loses much of its pungency.

The various grades of black tea are known as Orange Pekoe, Pekoe, Souchong, etc. These names formerly indicated that certain leaves (younger or older) were used, but they are now only commercial terms, having lost most, if not all, of their original significance.

[1] Katayama, T. On the aroma of black tea. Bull. Cent. Agr. Exp. Sta. **1**: 150. 1907.

Green tea differs from black tea in that fermentation is not allowed. To prevent this the leaves are rapidly heated as soon as picked. This is done by dry heat (*panning*) or by moist heat (*steaming*). After steaming the leaves are partially dried, then rolled, and then completely dried. The green color is often produced by rubbing the dried tea with a small amount of indigo and gypsum or other mixtures, such as greenish soapstone, but this practice is deprecated by the trade.

Oolong tea is made chiefly in Formosa and, to a less extent, in China and Japan. Its manufacture involves fermentation, but the process is not allowed to proceed for as long a period as in the manufacture of black tea.

The flavor of tea is due partly to an essential oil, which is one of the products of fermentation; its *stimulating effect* is caused by the presence of the alkaloid *caffeine* or *theine*.[1] The higher priced grades of tea are said to contain more theine than the lower.

The *pungency* of tea is due to the tannin which it contains. In the manufacture of black and oolong teas the tannin is oxidized by the fermentation, and it is the oxidized tannin that gives the color to the tea-infusion. One of the skillful points in the manufacture of these teas is to stop the fermentation at just the right stage to give the proper color to the infusion without sacrificing the pungency.

PAPAYA FAMILY

The commercially most important plant of the Papaya Family (*Caricaceae, Papayaceae*) is the Papaya (*Carica Papaya*), also called Papaw, or Pawpaw. There are in the genus some 20 species, usually dioecious. *Carica Papaya* is sometimes polygamous; that is, on a given tree some of the flowers are perfect and some either staminate or pistillate. In dioecious trees the staminate flowers are borne on long peduncles in the axils of the leaves, while the pistillate flowers are sessile in the leaf-axils. In the latter case the fruits are on short stems (Fig. 464), but the fruits of perfect flowers of polygamous trees hang on long peduncles (Fig. 465). The trees are seldom branched. This

[1] The alkaloids *caffeine* (from coffee) and *theine* (from tea) are practically identical, chemically.

species should not be confused with the North American Papaw, which is *Asimina triloba*, of the Anonaceae (p. 594).

FIG. 464.—Pistillate tree of the Papaya (*Carica Papaya*), showing the fruits on short peduncles. *Cf.* Fig. 465.

The fruit of the Papaya is used green as a vegetable, and the milky juice obtained from it is the source of the *papain* of com-

merce, a proteolytic enzyme sold in the form of a powder. It is intermediate in its action between trypsin and pepsin, and

FIG. 465.—Polygamous tree of Papaya (*Carica Papaya*), showing the fruits on the long peduncles of the perfect flowers. *Cf.* Fig. 464. (From plant in Brooklyn Botanic Garden Conservatories.)

is used in medicine as an aid to digestion. It is said that the leaves, which also contain papain, will make meat tender when boiled with it.

ST. JOHN'S-WORT FAMILY

In the St. John's-Wort Family (Hypericaceae) is the Mangosteen (*Garcinia mangostana*), one of the most highly prized of tropical fruits.

ORDER, Myrtales

The tropical plants of this order include numerous shrubs and trees, but in the temperate zone they are mostly herbs. The flowers are extremely variable in structure, usually with a four-parted calyx, four distinct petals, and an inferior ovary.

EVENING-PRIMROSE FAMILY

The Evening-Primrose Family (*Onagraceae*), contains the cultivated *Fuchsia*, so named after Leonhard Fuchs,[1] and the Evening-primroses, one species of which (*Oenothera Lamarckiana*) has become "immortalized" by the studies of Hugo de Vries,[2] which led to the formulation of the "Mutation theory" of the origin and kind of variations which de Vries considers furnish the material upon which natural selection acts and has acted in the past, in the evolution of new species (*Cf.* p. 1011).

The plants of the Evening-Primrose Family are herbs (rarely shrubs), having leaves without stipules. Glands often occur in the place of stipules. The pollen-grains are united by cobwebby threads. The slender single style bears a 2–4-lobed or capitate stigma. The fruit is either a pod or a small nut.

The genus *Oenothera* comprises herbs that are either annual, biennial, or perennial. The seedlings form a rosette of leaves, from the center of which leafy stems continue up to a height that varies from one to several feet, according to the species and the conditions of growth or of cultivation. The leaves are alternate on the stem, the yellow flowers are either axillary or in terminal spikes, and the erect buds open in the late afternoon,

[1] Leonhard Fuchs, author of one of the famous old herbals, *De historia stirpium* (1542), and of the *New Kreuterbuch* (1543), was born in Bavaria in 1501 and died in Tübingen in 1566. He was professor of medicine in the University of Tübingen (1535–1566).

[2] Hugo de Vries. Die Mutationstheorie. Leipzig, 1901–03. Eng. Tr. by Farmer and Darbishire, Chicago, 1909. Species and Varieties, their origin by mutation. Edited by D. T. MacDougal. Chicago, 1906.

the flowers closing early the next day—whence the name, Evening-Primrose.[1] The pollen-grains are loosely connected by cobwebby threads. The sepals usually fall off early (deciduous), and the elongated ovary is four-celled, developing, in the fruit, into a somewhat cylindric or slightly tapering capsule (Fig. 466).[2]

FIG. 466.—Lamarck's Evening-Primrose (*Oenothera Lamarckiana*). Upper portion of flowering stem, showing buds (at the top), flowers, and ripening ovaries (below), each in the axil of a bract. (After de Vries.)

MYRTLE FAMILY

The Myrtle Family (*Myrtaceae*) comprises shrubs and trees (rarely herbs) which are of economic importance either for their fruit or for the pungent aromatic, and volatile oil in which they

[1] One should not be misled by the common name evening-*primrose*. *Oenothera* is in no sense a primrose, botanically speaking; that is, it is not related to the genus *Primula*, which is in a different order (*Primulales*).

[2] We have described this plant in more detail than some other species because of the important rôle it has played during the past twenty years or more in the experimental study of evolution.

abound. The leaves are punctate with pellucid (translucent) dots. The 4–5 petals are inserted on the margin of a disc, or may be wanting. The stamens are usually numerous.

Among the economically important plants of this family are the following:

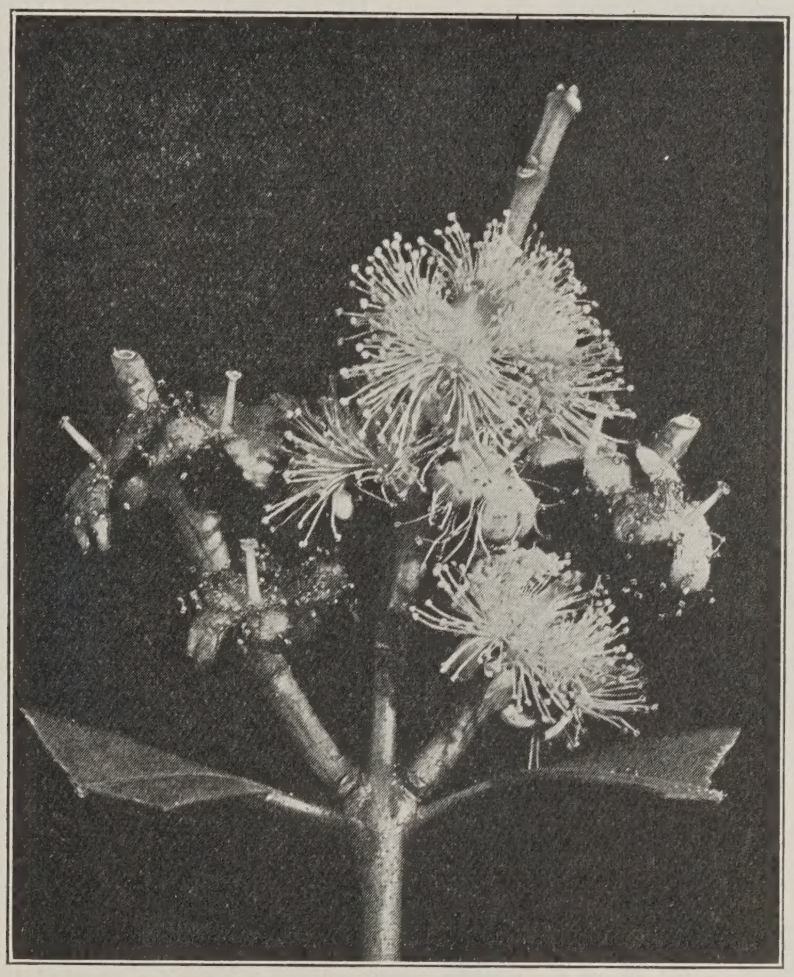


FIG. 467.—Flowering branch of the strawberry Guava (*Psidium cattleianum*).

Guava, various species of *Psidium*, including *P. cattleianum* (Fig. 467), and *Psidium Guajava* (Fig. 468). The fruit is a pulpy berry, with slightly acid juice, and numerous seeds. Guavas, introduced from the tropics, have become established in Florida and southern California. In Florida *P. Guajava* has escaped from cultivation and tends to become a pest. The fruit is used largely in making guava jelly and guava paste.

Cloves (*Eugenia aromatica* Baillon)[1] are native in the Moluccas, or Spice Islands, of the Malay Archipelago, and are cultivated in Amboyna, Sumatra, Zanzibar, Pemba (Africa), Madagascar and, to a less extent, elsewhere. According to Watt, the clove is not systematically cultivated anywhere in India, although it is traded in so extensively there as to make it one of the most important spices, and one likely to be cultivated in the future.

The "cloves" of commerce are the dried unexpanded flower buds of this plant (Fig. 469), and derive their name from their

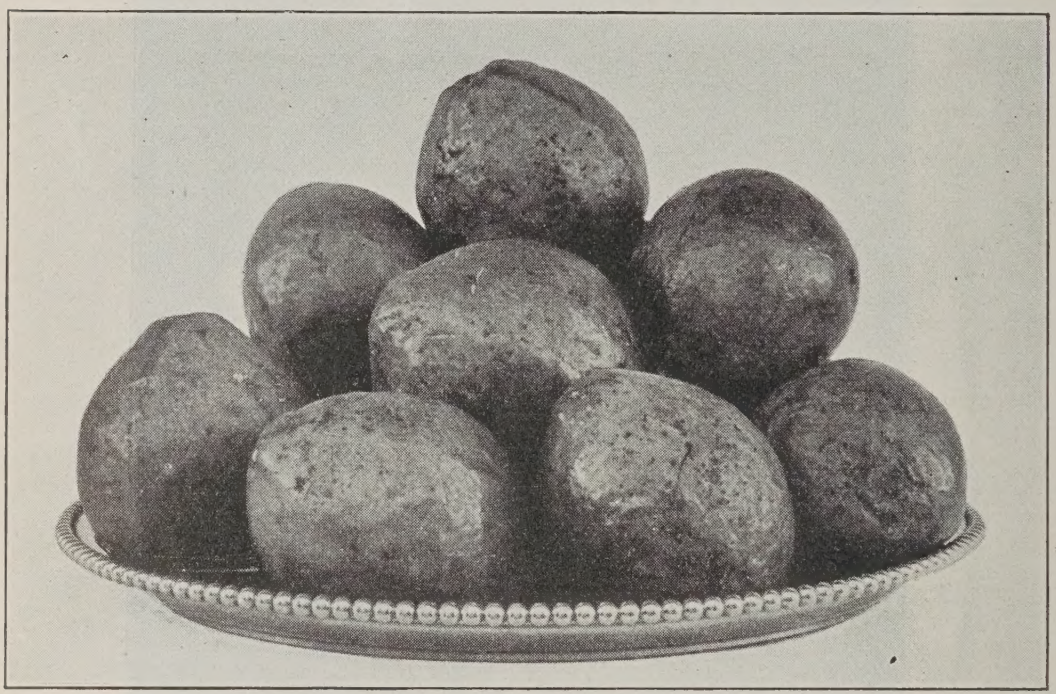


FIG. 468.—Fruits of the Common Guava *Psidium Guajava*). (After Popenoe. U. S. Dept. Agr.)

resemblance to a nail (Latin, *clavus*). The stalk of the clove is the immature ovary, at the top of which the corolla forms a little ball, surrounded by the four teeth of the calyx. If the buds are not picked the flower opens, pollination takes place, and the ovary develops into a juicy, purple berry, containing one or two seeds. This berry is called the "mother clove."

[1] The name *Eugenia* is from Prince Eugene of Savoy (1663–1736). *Linnaeus* (1753) called it *Caryophyllus aromaticus*, the name *Caryophyllus* (nut-leaf) referring to the nature of the commercial cloves, made up, in part, of the floral envelopes. The plant was called *Eugenia caryophyllata* by Thunberg, and *Jambosa Caryophyllus* by Niedenzu.

The tree is propagated by planting the mother cloves. The seeds do not germinate for about 5 weeks, and the seedlings are transplanted when about 4 feet high. They may also be propagated by layering. Young branches, when brought into

FIG. 469.—Flowering branch of the clove (*Eugenia aromatica*). An unopened flower-bud (clove) is conspicuous near the top. (After Maxon, U. S. Dept. Agr.)

contact with the soil, take root in about six weeks. The plants require shade for the first 2–3 years, but not thereafter. The yield begins at about the sixth year and reaches a maximum at about the 12th year, the average annual crop being about 6–7

pounds of dried cloves per tree. In Amboyna the trees do not begin to bear until about the 12th or 15th year, and may continue to bear for 75–150 years. In Sumatra, however, they bear only about once in three years and endure for only 20–24 years, depending on the richness of the soil. The trees are very shallow-rooted. The buds (first green, then yellow) are picked by hand as soon as they become bright pink or red in color, but they turn brown when dried. All parts of the plant contain the volatile, aromatic "oil-of-cloves" which is prepared for commerce by distilling the flower buds and flower stalks. It is a compound composed of "light oil of cloves" (caryophyllene), which comes over first in distilling, and *Eugenol.* Oil of cloves is extensively used in the preparation of plant tissues for microscopic study, in the manufacture of perfumery, and as an application to releave toothache. The oil is valuable in proportion to its Eugenol content (50–85%). The dried flower buds are used as a condiment.

Allspice, or Pimenta (Fig. 470), the fruit of *Pimenta officinalis,* also belongs to the Myrtaceae. It is indigenous to the West Indies and tropical America, being largely cultivated in Jamaica. The commercial product is the dried fruit or drupe. On distilling, allspice also yields a volatile oil that contains about 60% of eugenol.

Eucalyptus.—This genus is native in Australia and the adjacent islands of Tasmania, New Guinea, and others. Nearly all of the 150 or more species are found in Australia. The first botanical description of the genus was by the French botanist L'Hertier, in 1788, the first species to be described being *Eucalyptus obliqua.*

All the species are evergreen, some growing typically in forest groups, others scattered, some being dwarfed shrubs (known in Australia as "Mallees"), others being among the tallest trees of the world. Some species grow only in tropical lowlands, others in desert regions, and some in alpine environment. The trees are of very rapid growth. For example, studies made by Hall[1] in Uruguay in 1900 revealed that an unnamed species of *Eucalyp-*

[1] Hall, C. E. Additional notes on tree measurements. Trans. & Proc. Bot. Soc. Edinburgh **214**: 243–258. 1900. (Exp. Sta. Record **12**: 1048. 1901.)

tus in that region had, in nine years, an average annual growth in circumference of trunk of 108 mm., while in the same region and period of years the average annual growth in circumference of Poplar (*P. fastigiata*) (one of the fastest growing trees of the United States) was only 18–22 mm., of the locust (*Robinia Pseudacacia*) only 11 mm., and of an Oak only 27–44 mm.

FIG. 470.—Flowering branch of Allspice (*Pimenta officinalis*), ½ natural size. (After Baillon.)

Near Santa Barbara, California, are trees of the Blue Gum (*Eucalyptus globulus*) only 25 years old, which are as large as oaks that are known to be 200–300 years old. In the brief space of 20 years they may become large enough to yield lumber for railroad ties, telegraph poles, and innumerable other commercial uses. The Blue Gum "suckers" freely, and when a tree only

FIG. 471.—*Eucalyptus globulus.* Portion of flowering branch. In the upper left hand flower-bud the lid (calyptra) of the calyx has just been loosened. In the adjacent bud and the lower left hand bud the lid has fallen away.

8–10 years of age is cut off near the ground it will produce suckers 75–100 feet high in from 6–8 years.[1]

The inflorescence may be axial or terminal or both. The flowers occur either singly or in paniculate umbels, which are at first enclosed in a pair of small bracts that early fall off. The calyx varies much in size, and its upper portion is transformed into a deciduous calyptra or lid (Fig. 471). It was this latter feature that led L'Hertier to call the genus *Eucalyptus*.[2] There are no petals, the stamens are numerous in several rows, with threadlike filaments, and the long style is terminated by a flat or convex stigma. The lower part of the 2- to 6-celled ovary is adnate to the calyx tube. The ovules are numerous in each cell, but most of them remain unfertilized and therefore do not develop into true seeds, but only into seed-like bodies, smaller and of lighter color than the true seeds.

The lanceolate or sickle-shaped leaves may be either alternate or opposite and in some species the first leaves are opposite and the latter ones alternate. They usually have long petioles, but in some species they are sessile. The leaf-blades are placed in a vertical plane and consequently the tree affords little shade. The leaves also twist on their petioles, and this is thought to keep the thicker cuticle toward the sun, and thus to reduce the loss of oil by volatilzation. The blades are glabrous and thick and, as in other families of the Myrtales, are dotted with either pellucid or concealed glands which secrete the well-known Eucalyptus oil.

The eucalypts have been a very difficult group to classify, not so much because of the large number of species, but because much of the early work was done with herbarium specimens which suggest an apparent gradual transition from one group to another. When herbarium study is supplemented by field work this apparent transition is not confirmed.[3]

[1] McClatchie, A. J. Eucalypts cultivated in the United States. U. S. Dept. Agr. Bur. For. Bull. 35. 1902.

[2] *Eucalyptus*, from the Greek εὖ (*eu*), *well*, and καλύπτειν (*kaluptein*), *to cover*, since the lid well covers the calyx until the stamens are mature.

[3] Baker, Richard T, and Henry G. Smith. A research on the eucalypts, especially with regard to their essential oils. Technical Museum, New South Wales Tech. Education Series, No. 13. Sydney, 1902.

The importance of studying plants in the field as well as from herbarium specimens finds striking emphasis in the systematic study of the eucalypts. In fact Dr. Woolls, the author of the *Flora of Australia,* states that trees of this genus "placed by

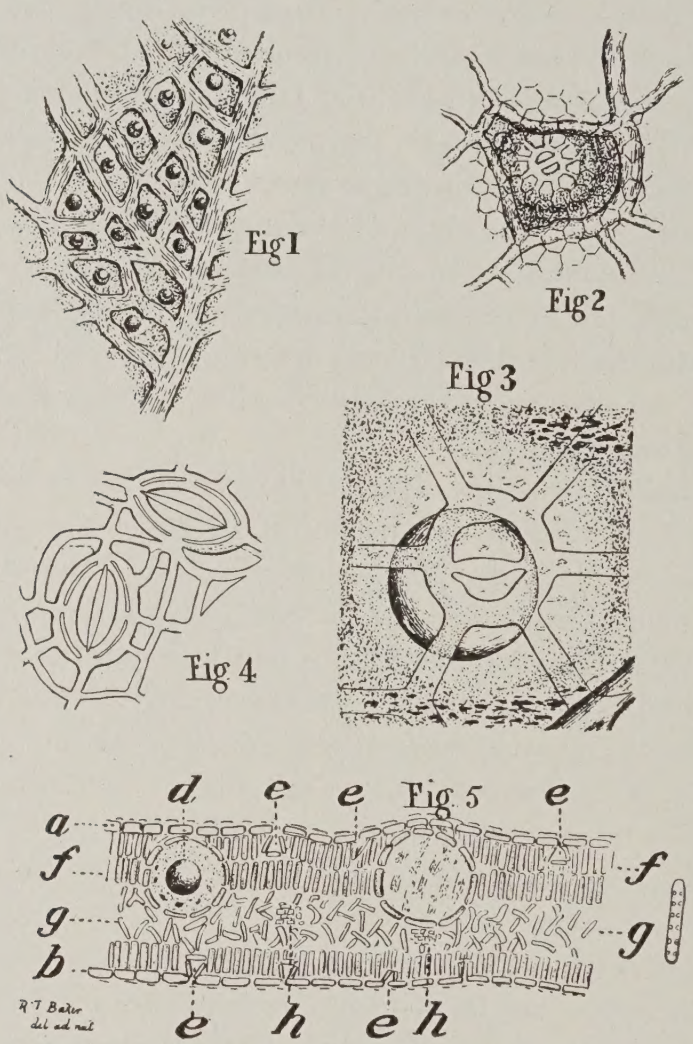


FIG. 472.—*Eucalyptus punctata.* 1. Part of leaf with lower epidermis removed, showing oil-glands—some with the oil-globule, some without it; 2, An empty oil-gland more highly magnified than in 1; 3, Portion of 2 still more highly magnified. The sphere represents an oil-globule enclosed in an oil-cell; 4, Stomata; 5, Cross-section of the leaf. *a*, upper epidermis; *b*, lower epidermis; *c*, oil-cell empty; *d*, oil-cell containing globule of oil; *e*, stomata; *f*, palisade parenchyma; *g*, spongy parenchyma; *h*, small vascular bundles. (After Baker and Smith. Technological Museum, New South Wales.)

botanists under one specific name would never be so considered if studied in Nature, for there the specific differences are so marked that no one would even think the trees were one and the same species."

It has also been found impossible to establish reliable species on structural characters alone, but the species based upon the chemical composition of the oils, dyes, and tans, taken in connection with the morphological characters are found by Baker and Smith to be clearly defined and constant.

There is a correlation between the morphological characters of the leaves and the amount and chemical composition of the oil secreted by the glands in the leaves (Fig. 472). In certain species *pinene* is the chief constituent of the oil, with *eucalyptol* and *phellandrene* absent or present only in small amount, while in other species phellandrene predominates to the partial or total exclusion of the other constituents. When eucalyptol predominates the lateral leaf-veins become more open, and a few of them stand out in greater prominence than the others. The open venation is correlated with the formation of a larger number of oil glands. A few species do not yield any oil.

The trees known in America as "Blue Gum" and "Red Gum" are, respectively, *E. globulus* (Fig. 471) and *E. rostrata*. The genus has been introduced all over the world wherever the climate is favorable to its growth. It has been stated that "more trees of this genus have been planted away from its original habitat than of all other forest trees combined." The genus is said to have been first introduced into America (California) in 1856, in which year 14 species were planted.

The Eucalypts have more economic uses than any other genus of trees, with the possible exception of certain palms. They serve as forest cover and wind breaks, and for ornament and shade; they yield invaluable oils, gums, and resins; the wood is used for timber and fuel; the flowers furnish abundant nectar for bees.

The Myrtales also include the following families of plants, of minor importance commercially, but of economic interest.

POMEGRANATE FAMILY

The Pomegranate Family (*Punicaceae*) includes small trees and shrubs with leaf blades entire, flowers perfect and showy, and either clustered in the leaf axils or solitary; sepals and petals 5–7; the wrinkled petals and the numerous stamens are inserted on the throat of the leathery hypanthium which is adnate to the

ovary. The pistil is composed of several carpels united. The one-celled ovary contains numerous ovules, and ripens into a very seedy, leathery fruit, which is a berry, crowned with the calyx (Fig. 473). The seeds are surrounded by a watery pulp. The *pomegranate* of Biblical and modern times (*Punica Granatum*) is found wild in Persia, where it is probably native, and in southern Europe. It has become naturalized as an escape from cultiva-

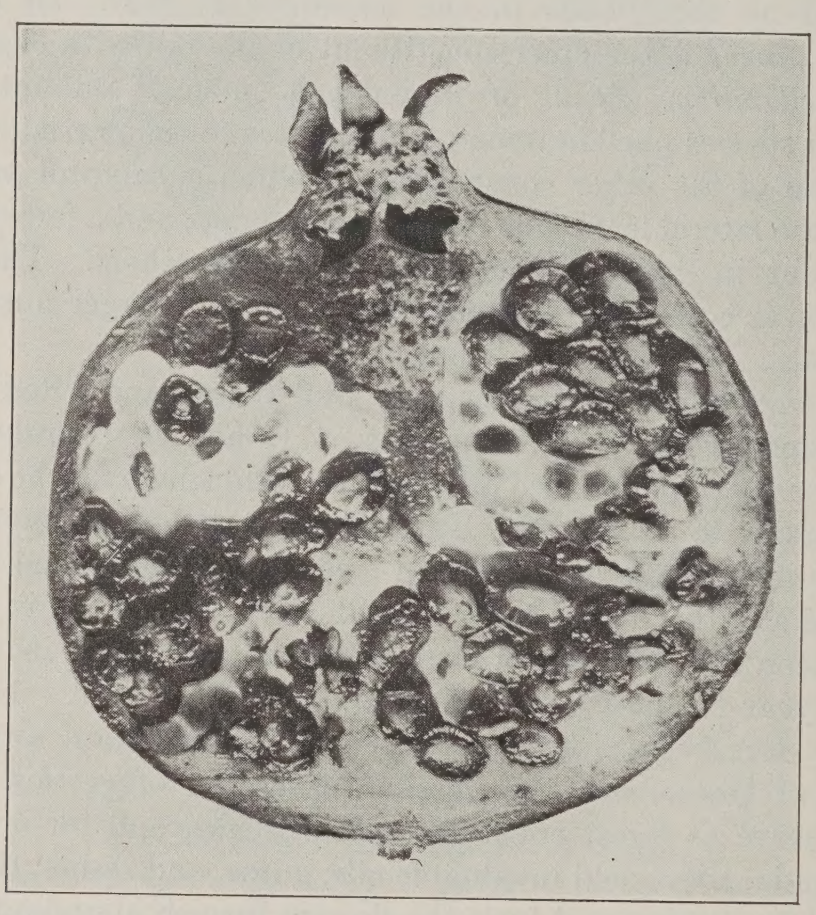


FIG. 473.—Pomegranate (*Punica Granatum*). Longitudinal section through the fruit. Above are three of the thick, persistent sepals surrounding the withering petals and stamens. The style is also seen projecting from the ovary-wall.

tion in northern Africa, Florida, and other warm countries. Its cultivation dates from prehistoric time. The Hebrews learned of it during their captivity in Egypt, and found it growing in Palestine on their return thither. It was known to the Greeks of Homer's time, and is frequently mentioned in the myths of ancient Rome. In Pliny's time the best pomegranates came from Carthage, and hence were called "Punic apples" (*Mala punica*),

whence the generic name of the plant.[1] Fossilized leaves and flowers of a pomegranate have been found in the strata of the Pliocene epoch. The fruit has now become fairly common in the markets of the United States.

FIG. 474.—Mangrove (*Rhizophora Mangle*) and, at the right, the Black Mangrove (*Avicenna*), of the Verbena Family. North shore of western Cuba.

MANGROVE FAMILY

The Mangrove Family (*Rhizophoraceae*) is a small family, comprising about 15 genera and some 50 species of trees and shrubs found only in the tropical or sub-tropical regions of both hemispheres. There are two Old World species, inhabiting the coastal regions of tropical Africa, Australia, and the East Indies. In the New World the only representative of the family is the Mangrove

[1] The specific name is that by which the fruit was designated in classic Latin—*granatum*, from the adjective *granatus* (having many seeds). The common English name, pomegranate, has the same meaning, *i.e.*, seedy apple.

(*Rhizophora Mangle*), which is known also as the Red Mangrove. It grows on the coast of the West Indies (Fig. 474), on the Florida Keys, and along the shores of streams and on the coast of the southern part of the mainland, being confined to salt or brackish water. The tree is evergreen, with the opposite, entire leaves rather leathery. The perfect flowers grow in clusters of two to

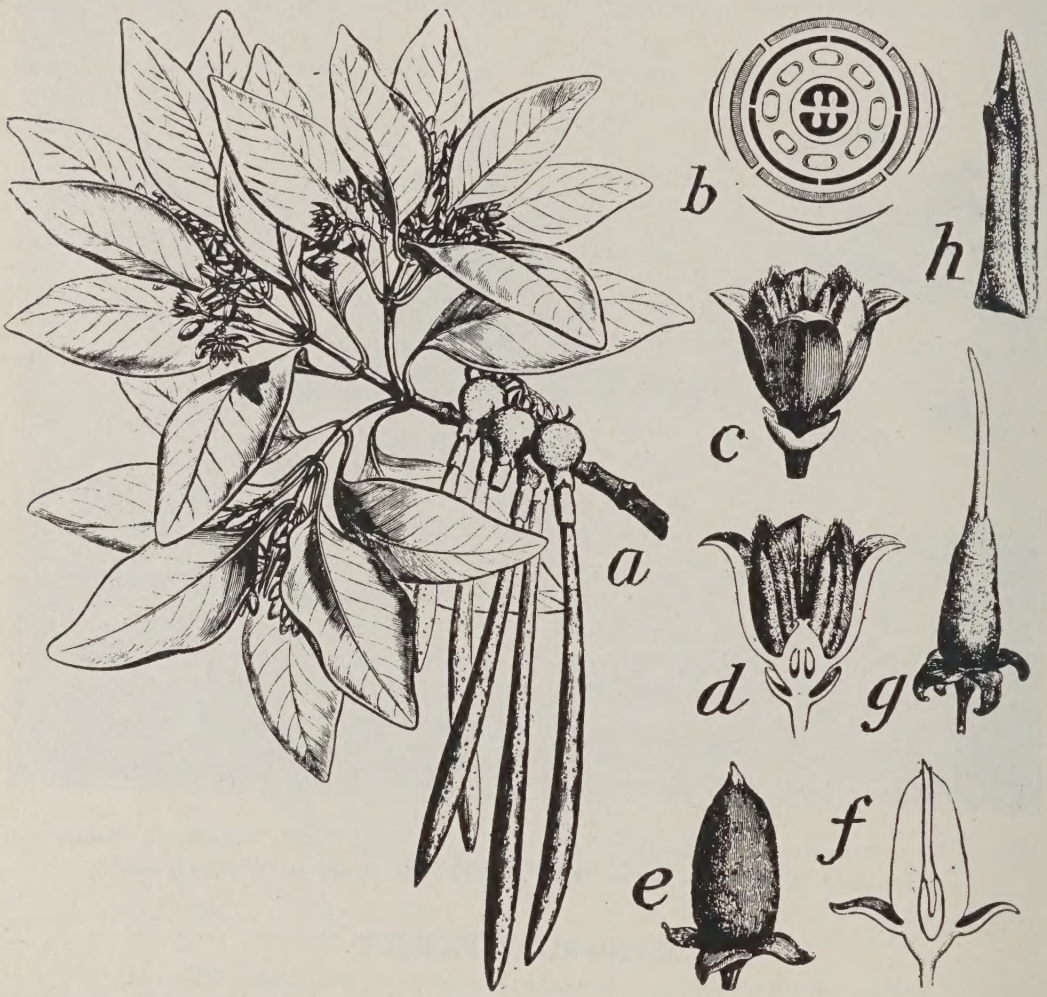


FIG. 475.—Mangrove (*Rhizophora Mangle*). Flowering branch, with germinating seeds, and details of flower and fruit. (After Baillon.)

several, and the 4 sepals and 4 pale yellow petals, like the leaves, are leathery. There are 4–12 stamens, and the inferior, two-celled ovary matures into a cone-shaped, leathery berry, crowned with the leathery calyx, with reflexed sepals (Fig. 475).

Only one ovule of the two-celled ovary matures into a seed. The fruit never dehisces, and the seed germinates within the ovary, while the fruit is attached to the tree. The nucellus and outer

seed-coat are completely digested and absorbed as nourishment for the large endosperm that forms within the embryo-sac. The young embryo develops in the micropylar end of the endosperm. According to Cook,[1] the growth of the embryo is divided into three periods: (1) the first growth of the cotyledons, (2) the growth of the hypocotyl, (3) the second growth of the cotyledons.

The outer layer of cells of the cotyledons is transformed so as to resemble a glandular epithelium, as in the case of the cotyledon of the corn grain (p. 192), and by the action of these cells the cotyledon, as it grows, absorbs the tissue of the endosperm, and this material is then transferred to nourish the large and rapidly growing hypocotyl. As the cotyledon continues to increase in size it pushes the tip of the hypocotyl with the surrounding endosperm out through the micropyle of the seed into the cavity of the ovary. There is no rest-period (*Cf.* p. 788).

The now well nourished hypocotyl begins to grow rapidly in thickness and length, and then, by elongation of the cotyledons, ihe summit of the hypocotyl, where the cotyledons are attached, is pushed out beyond the tip of the ovary. Covered with the pendent hypocotyls, the trees present an unusual sight, appearing to bear many dangling roots. It is this feature which gave the name Rhizophora to the genus.[2] An abscission layer finally forms at the zone where the cotyledons are attached to the hypocotyl, and the latter drops off. At this stage of development the hypocotyl may be from four to ten inches long, and one-half to three quarters of an inch thick. Since the hypocotyl is thickest and heaviest in its lower one third, it always falls vertically, and this fact, combined with its weight, results in its becoming firmly anchored in the mud. It will even remain vertical when passing through 2–3 feet of water before reaching the surface of the mud.

Once imbedded in the soil the plumule begins to develop into an aerial leafy shoot, and roots begin to grow out, not only from the hypocotyl, as in most plants, but also from the epicotyl, thus

[1] Cook, Melville Thurston. The embryology of Rhizophora Mangle. Bull. Torrey Bot. Club. **34**: 271–277. 1907.

[2] *Rhizophora*, from two Greek words ῥίζα (*rhiza*), root + φέρειν (*pherein*), to bear, meaning root-bearing. The specific name, *Mangle*, is the local Spanish name for the mangrove.

more firmly anchoring the plant, as well as supplying it with an abundance of water and nourishment. Everything seems to be planned with a view to insuring the anchorage of the plant in the place where the seed falls.[1] An old tree is thus commonly surrounded by many seedlings. If the water is too deep the young seedling, failing to penetrate the mud, is buoyed up to the

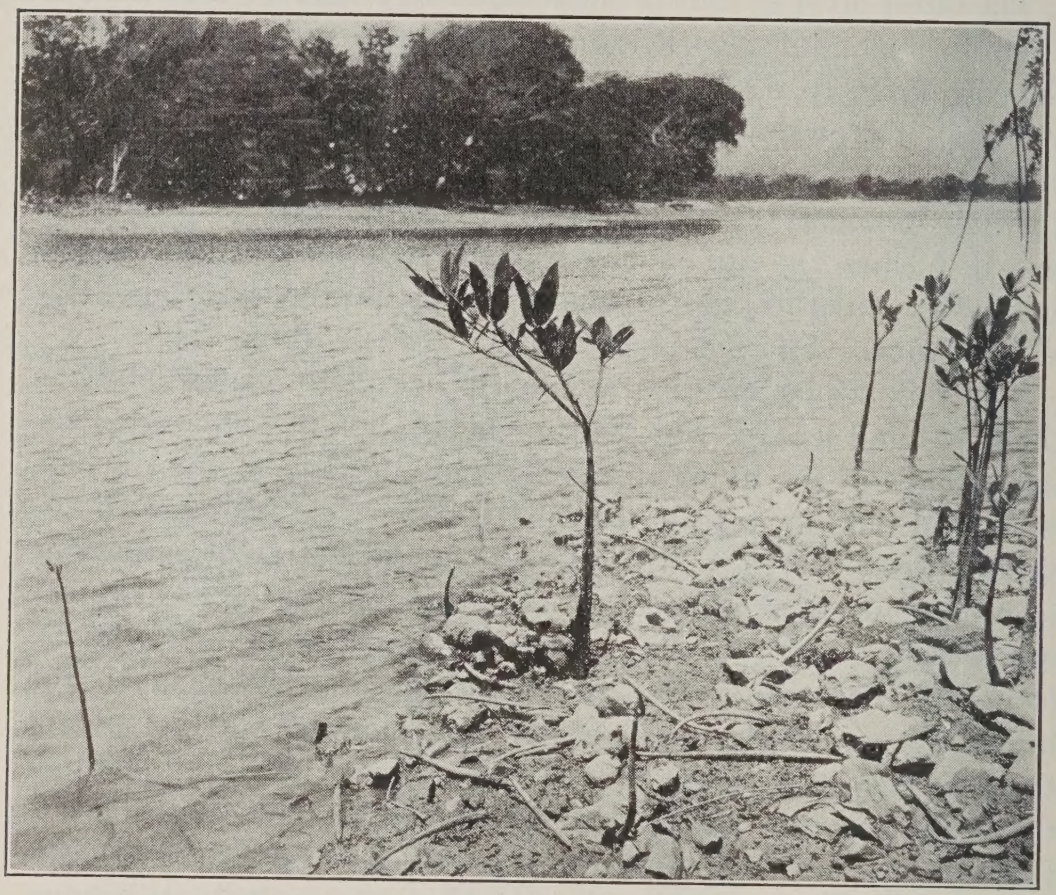


FIG. 476.—View on the edge of a mangrove swamp. Young mangroves and recently fallen seedlings looking (in the picture) like round sticks. (Photo by G. V. Nash. Courtesy of the New York Botanical Garden.)

surface of the water and carried by the currents to some other resting place, where it gains a foothold and becomes the center of a new colony (Fig. 476). Of course some of the seedlings never do become rooted, and so perish.

[1] It is interesting to note the contrast, pointed out by Kerner, between the mangrove and the ginkgo in the manner of seed maturity. In the ginkgo the seed falls from the tree while the embryo is in the very earliest stages of its development.

It is on this "viviparous" habit of the tree that its chief economic value rests, for it is one of the most important agents in the formation of new land in the coastal regions where it grows. This result is brought about by the peculiar root-system of the plant, for it sends out roots into the air from its spreading branches, and these roots, penetrating the soil, form a thick network which becomes the lodging place of silt, decaying vegetation, and every floating thing brought along by tidal and other currents. To this flotsam are added the leaves and branches that fall from the tree itself, resulting in a slimy bottom which, in the course of years, rises well above the level of the water, and becomes dry land, available for agriculture. This very process results in the death of the trees, for they like a wet soil, and so the line of living trees continually advances farther out from shore. By the agency of the mangrove many islands have been built up in the shallow water around the Florida Keys, and in time these become tied to the mainland, which is also extended in a similar way. As a builder of land the mangrove is hardly second in importance to the more famous coral polyp.

The bark of the mangrove yields tannin, but has not, as yet, become commercially important in this connection.

ORDER, Umbellales

The *Umbellales* comprise three families, viz., the Dogwood Family (*Cornaceae*); the Ginseng Family (*Araliaceae*), which includes the American Spikenard (*Aralia racemosa*), wild Sarsaparilla (*Aralia nudicaulis*), and the Ginseng (*Panax quinquefolium*); and the large Parsley Family (*Umbelliferae*), all characterized by having their flowers usually in umbels, a single whorl of stamens, an inferior ovary, and a single seed-coat. These four characters, occurring together, sharply differentiate the *Umbellales* from the other Polypetalae. This combination of characters is also found in the sympetalous order, *Rubiales*.

In the Parsley Family are the important crop plants, Parsnip and Carrot, the garden plants, Celery, Parsley, and Caraway, and the wild plants from which the cultivated forms were derived.

GINSENG FAMILY

The Ginseng Family (*Araliaceae*) includes trees, shrubs, and herbs. The flowers with 5 sepals and petals and 5 stamens,

resemble those of the Parsley Family except that they usually have more than two styles and more than two cells to the ovary

FIG. 477.—Flowering plant of Ginseng (*Panax quinquefolium*). (Photo by E. M. Kittredge.)

(and fruit). The fruit is a drupe with few to several cells. Of some 52 genera and 450 species the more important are *Aralia*, *Hedera*, and *Panax*.

Aralia includes the Hercules' Club (*A. spinosa*), often used in ornamental planting, and having very large, thrice compound leaves (Fig. 33); Wild Sarsaparilla (*A. nudicaulis*); the Wild Elder or Bristly Sarsaparilla (*A. hispida*); and the American Spikenard or Indian Root (*A. racemosa*).

Hedera Helix is the True or English Ivy, a woody climber of beautiful evergreen, glossy leaves, 3-angled or 3-lobed, or, in some varieties, 3-cleft. The yellowish green flowers are followed by blackish berries, and the plant is much used as a wall-climber. It adheres to walls by aerial roots, and does specially well on shaded or protected walls. It is liable to winter-killing in the northern United States.

The economically most important genus is *Panax*, which includes the Ginseng, *Panax quinquefolium* (Fig. 477). Its flowers are polygamo-dioecious on a simple, terminal, solitary umbel; the fruit, red. The plant is a perennial herb, with a deep, tuber-like, rootstock, spindle-shaped, and often branched. The simple, erect, annual stem bears one whorl of three palmate leaves. The species prefers cool, rich woods, and when cultivated is best grown under artificial partial shade.

The name *Panax* is from the Greek word meaning "cure all," the same word from which the English word *panacea* is derived. This name refers to its reputed value as a medicine. For this it is prized chiefly by the Chinese (together with its Asiatic relative, *P. ginseng*). The root is seldom used medicinally in America, but large quantities of the root of the American species are exported annually to China.

In earlier days a plant was supposed to have medicinal value if one of its organs resembled a man or an organ of the human body. Thus liverwort (*Hepatica*) was supposed to be good for the liver because its leaves were (roughly) liver-shaped. So the medicinal value of ginseng is said to have been imputed to it through the resemblance of its tuberous root to the human body, or to the human thigh. The name, ginseng, is from the Chinese *jin-tsan* or *jin-shen*, said by some to mean "resembling a man." Other students of Chinese, however, state that the Chinese words mean "the first (or most important) of plants."

Acanthopanax pentaphyllum is an effective shrub for unclipped hedges.

PARSLEY FAMILY

Common or garden Parsley (*Petroselinum hortense*), cultivated chiefly for its leaves which are used for flavoring and as a garnish, is frequently found as an escape. It is native to the Mediterranean region. The plant was known to the ancient Romans under the name *apium*. The genus name, *Petroselinum*, means "rock celery." It was used for the victor's crown in the ancient Nemean games. Old seeds of parsley germinate more readily than new seeds, while the opposite is true of the related genus, celery. This fact was known over 200 years before Christ by Palladius, who also described a method of getting a curled variety from the plain-leaved form. The curled variety was under cultivation in America at the beginning of the nineteenth century.

FIG. 478.—Celeriac, (a form of *Petroselinum graveolens*). (After Vilmorin, from Robbins.)

Celery (*Petroselinum graveolens*),[1] is among the oldest of cultivated plants. It is mentioned by Homer, who called it *sélinon*, whence our name, celery. It is cultivated for its leaf-stalks, eaten both raw and cooked. As is well known, the stalks are made tender by bleaching, or blanching, which is accomplished with some varieties by "banking"—that is, by starting the plants in a shallow trench, and then banking the soil up around them as they grow, thus excluding the light and preventing the formation of chlorophyll. Celery takes kindly to the increased moisture resulting from the trenching, and in this it resembles many Umbellifers which thrive in damp places.

Celery develops a long taproot. When young seedlings are transplanted this is broken, and a mass of fibrous roots is formed. If transplanting is delayed too long the plant suffers because the

[1] The generic name applied by Linnaeus to parsley and celery was *Apium*, a name still used by some.

taproot has penetrated deeply into the soil and few side roots have formed. It has a wide range, being found from Scandinavia to North Africa and, in Asia, from the Caucasus to the mountains of British India. One type (*Celeriac*) is cultivated for its fleshy root, which is eaten cooked (Fig. 478). Plants protected by boards or paper, instead of by hilling, seem to be more apt to suffer from fungous diseases, especially when the weather is warm and humid. Some varieties are more or less perfectly self-blanching, without protection by hilling or otherwise. Harvey has recently found that celery can be satisfactorily blanched by applying acetylene, or preferably ethylene, gas in the field.

The Parsnip[1] (*Pastinaca sativa*) has compound umbels of yellow flowers, in contrast to parsley and celery which have white flowers. The calyx teeth do not develop, or only slightly. Even in the very young seedling the hypocotyl and taproot begin to thicken, and this ultimately forms the edible parsnip of our tables. The wild plant, a biennial or rarely an annual naturalized from Europe, is a common weed along roadsides and elsewhere in the eastern United States, and all varieties of garden and field parsnips are believed to have originated from this plant. In fact, forms closely resembling the cultivated type can readily be produced by selection in breeding the wild plant. The plant (Fig. 479) has been under cultivation since the time of the ancient Greeks and Romans. It has been grown in the United States (Virginia) since about 1600.

The wild Carrot (*Daucus Carota*), naturalized in the United States from Europe, is the original of the cultivated form, and often becomes a very troublesome weed in fields and waste places. The genus contains about 25 species of wide geographical distribution. It is an annual or biennial with leaves pinnately compound, and the white, rose-colored, or pale yellow flowers are in compound umbels which, as they mature, become strongly cup-shaped, the flowers bending over in as the fruit sets. The flowering period extends from June to September. One or more of the central flowers or florets of each umbel is commonly very dark purple. In some cases an entire umbellet is transformed either into one unusually large purple flower, or into numerous

[1] From the Latin verb, *pastinare*, meaning "to dig or trench the ground"

smaller and lighter colored ones. Sometimes two umbellets are thus transformed.

The great French nurseryman and breeder, Vilmorin,[1] secured fairly good garden varieties from the wild form by selection in only three or four generations from the wild plant. The "carrot" itself (fleshy root), as it matures, is drawn down into the soil by contractile roots, often aided by the contraction of the hypo-

FIG. 479.—Leaf and inflorescence of Parsnip (*Pastinaca sativa*). (After Robbins.)

cotyl itself (*Cf.* p. 107). In the wild carrot, food is stored in the hypocotyl-root in the form of starch, but, in the cultivated varieties, the carbohydrate is almost always stored in the form of sugar. The "carrot" contains a larger percentage of water (86%–88%) than does the parsnip, which has a higher food value than most of the "root" crops.

[1] Vilmorin, Pierre Louis François Levêquede. Le bon jardinier. 1836, p. 16; 1840, p. 195.

CHAPTER XXXIII

SYMPETALOUS DICOTYLEDONS

In all the preceding orders the flowers have petals not united, that is, they are apetalous or polypetalous; in the remaining dicotyledonous orders the flowers commonly have their petals more or less united—*sympetalous* or *gamopetalous*. This character differs, however, in different orders, from loose coherence or even entire lack of it (Primroses, Heaths, Milkweeds, Cucurbits, and others) to complete fusion, as in the tubular corollas of the bindweeds, morning-glory, figworts, and composites. In a few species (*e.g.*, American Ash) the corolla is wanting.

ORDER, Ericales

The order Ericales derives its name from that of its principal family—the Heaths (*Ericaceae*). These plants generally prefer an acid soil, and many of them thrive in bogs.[1]

HEATH FAMILY

In the Heath Family and the Blueberry Family (following) there are two whorls of stamens from the receptacle, and the anthers have terminal pores. The Heath family has a superior ovary, with the fruit usually a capsule, while the Blueberry has an inferior ovary, with the fruit a berry. They are chiefly northern plants, and are often grouped as one family (*Ericaceae*).

Erica, the heath, from which the family and order are named, comprises 500 or more species, some hardy and some (from South Africa) tender and grown, in America, only in conservatories. They are branching woody plants from 6–12 inches or more in height. The leaves are usually three-sided (rarely flat) with margins revolute, and occur in whorls of three to six. The 4-parted calyx is free, and the 4-lobed, white, rosy, or yellow, more or less bell-shaped corolla is hypogynous, and falls off early

[1] A bog has an inlet but no outlet, and the water and soil are rich in humic acid. A *swamp* has both inlet and outlet and the water is sweet.

(*i.e.*, early deciduous). There are eight stamens, and the ovary (sessile or rarely stalked) commonly has four cells, or rarely eight. The seeds are very small. One of the most popular of the hardy heaths is *Erica carnea*. The Cornish Heath (*E. vagans*), reaches a height of 3–4 ft. in England. The plant offered for sale by florists at Christmas time (often under the name of heather) is probably *E. melanthera*.

Calluna is the true Heather (Fig. 480). Its generic name is from a Greek word meaning to sweep, since its branches are

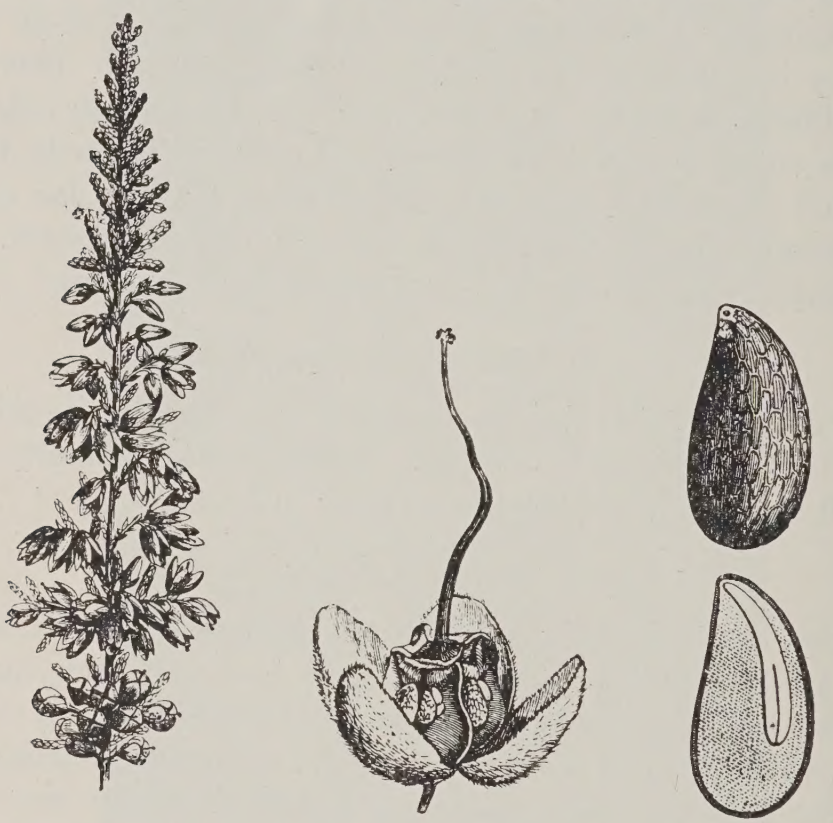


FIG. 480.—Heather (*Calluna vulgaris*). Flowering branch, dehiscent fruit, seed and longitudinal section of the seed, showing the embryo. (After Baillon.)

often tied together to make a sort of broom. In contrast to *Erica* the leaves are flat or scale-like, and occur opposite each other in four vertical rows. Also in contrast to *Erica* the colored calyx is deeply 4-lobed, and is longer than the 4-lobed corolla. There is only one species, *Calluna vulgaris* Salisbury (=*Erica vulgaris* L.); this is hardy, and has numerous horticultural varieties.

Rhododendron.—The name is formed from two Greek words meaning "rose-tree," in allusion to the beautiful flowers. As

many as 350 species are known, and many hybrid horticultural varieties, all grown as ornamental shrubs, valued for both flowers and evergreen foliage. The genus is widely distributed in the north temperate zone, and the mountains of tropical regions in the northern hemisphere. Its chief center is in the Himalayas and in Central and Western China. The plants do best in partial shade, and protected from high winds. The leaves are alternate and leathery, and the perfect flowers are borne in terminal clusters. The persistent calyx has 5 sepals, and the bell-shaped, colored corolla has 5 lobes, the two lower not spreading as much as the three upper (Fig. 481). There are usually 10 stamens, and the ovary is 5–20 celled. The large, conspicuous flower buds are fully formed by fall.

FIG. 481.—Flower of *Rhododendron* (left), and of *Azalea* (right). (After Baillon.)

Rhododendron maximum, known as the Great Laurel, grows wild from Nova Scotia to Georgia, flowering in June and July, and several varieties are recognized. One of the most beautiful species is *R. catawbiense*, native from Virginia to Georgia, but hardy as far north as New England. *R. arboreum*, an Himalayan species, may become a tree 40 feet high. Many beautiful varieties have been produced by crossing *R. arboreum* with a hybrid resulting from a cross between *R. catawbiense* and *R. ponticum*.

Azalea is not recognized as a separate genus by some botanists, but others place in this genus all "rhododendrons" having deciduous foliage. The corolla (Fig. 481) is funnelform rather than campanulate as in rhododendron, and all the five lobes are spreading. There are rarely more than 5 stamens, and the ovary usually only 5-celled. The distinction between *Azalea* and *Rhododendron* is fairly clear if one considers only the American species, but in Asia, where these plants are most richly developed,

there are many forms having the characters of both groups, and no clear distinction is possible.

Azalea nudiflora, common in shady places from Maine to Illinois and south to Florida and Texas, blooms before the leaves appear. It is variously known as Pinxter and Wild Honeysuckle. *Azalea viscosa*, having a similar range, but largely confined to swampy places, is known as the Swamp Honeysuckle. *Azalea canescens* is the Mountain Azalea. *Azalea lutea*, the Flame *Azalea*, widely planted, is wild in dry woods from New York to Pennsylvania,

FIG. 482.—Mountain Laurel (*Kalmia latifolia*). Note the anthers resting in the pouches of the sympetalous corolla. (Photo by E. M. Kittredge.)

and in the mountains as far south as Georgia and Alabama. One of the most beautiful Asiatic species is *A. Hinodigiri*, with its abundance of scarlet flowers. Others familiar in cultivation are *A. ledifolia*, *A. mollis*, and *A. indica*.

Kalmia has seven or eight known species of evergreen shrubs or trees, seven of which are North American, the other Cuban. *Kalmia latifolia* is the Mountain Laurel or Calico Bush, so called from the color pattern of its corolla. *K. angustifolia* is the Sheep Laurel or Lambkill. The saucer-shaped corolla of all species has ten pouches and keels (Figs. 482 and 483). As the flower-bud

opens the anthers remain in the pouches, the filaments curving outward. When the flower is fully opened the anthers are easily

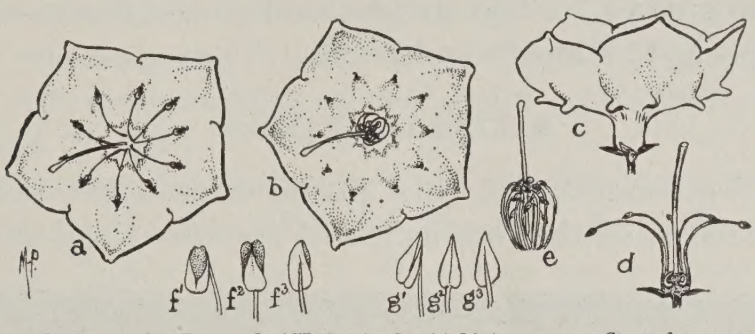


FIG. 483.—Mountain Laurel (*Kalmia latifolia*). *a*, reflexed stamens in their original position in the fully opened flower; *b*, stamens released and inflexed (detail at *e*); *c*, side view of perianth, showing the pouches of the corolla. *d*, essential organs; *f* and *g*, stamens.

dislodged from the pouches, and the filaments spring over in, scattering the pollen, and dusting any bee or other insect that may have alighted on the flower.

FIG. 484.—Trailing Arbutus (*Epigaea repens*). (Photo by E. M. Kittredge.)

The well-known Trailing Arbutus or Mayflower (*Epigaea repens*), common from Newfoundland to Saskatchewan, Wiscon-

sin, Michigan, Kentucky, and Florida, is also in the Heath Family (Fig. 484). Its generic name is from the Greek meaning "upon the ground." The species tends to be dioecious, and is dimorphous as to stamens and pistil.

BLUEBERRY FAMILY

In the *Vacciniaceae* the chief plants of economic importance are the Blueberries, the Cranberries (*Vaccinium*), and the Huckle-

FIG. 485.—Blueberry (*Vaccinium corymbosum*) in flower. (Photo by E. M. Kittredge.)

berries (*Gaylussacia*). The chief difference between the blueberries and huckleberries[1] is that in the former (*Vaccinium*), the ovary is only 4–5 celled, and the fruit is a many-seeded berry, while in the latter (*Gaylussacia*) the ovary is 10-celled, and the fruit is a berry-like drupe with 10 nutlets, usually not as sweet as are the blueberries (Figs. 261 and 485). The huckleberries *seem* the more "seedy" of the two when eaten, although as a matter of fact there are more seeds in the blueberries, but they are smaller and are enclosed in a relatively greater amount of soft

[1] The names are often used loosely or interchangeably.

tissue. We have spoken elsewhere of the great improvement in the size and other characters of the High-bush or Swamp Blueberries (*Vaccinium corymbosum*), brought about by cross-pollination and selection, and making them a profitable crop-plant that may be grown successfully on acid soil not otherwise of agricultural value (p. 368).

The cranberries of commerce are *Vaccinium macrocarpon, i.e.*, "the large fruited *Vaccinium*." There are two other species in the eastern United States, *V. Oxycoccus* and *V. erythrocarpum*, which have little or no commercial value. *V. erythrocarpum* is a low shrub with deciduous leaves, whose berries turn from light red to purple on ripening. The other two species are creeping or trailing plants, with small evergreen leaves, white beneath, and with red, acid berries. The persistent calyx tube is almost hemispherical, and adnate to the ovary, with the limb 4–5-cleft. The corolla is deeply four parted, with narrow and reflexed lobes or petals.

The stems form long, slender, trailing vines bearing evergreen leaves, the white-petaled flowers giving place to the large red berries which ripen in late September. The plant is said to have been originally called "crane-berry," from the fancied resemblance of the curved flower stalk and bud to the neck and head of a crane. The name cranberry would thus appear to be merely a shortening or corruption of craneberry.

The cranberry, found wild only in the cooler regions of North America, forms the most important crop of Cape Cod, growing in the sandy bogs. From Massachusetts, cranberry culture has been introduced into New Jersey, Wisconsin, and Nova Scotia.

Of numerous varieties, the most valued are the Late Howe (October), the Early Black (early September), and the Matthew. The varieties differ in the shape, size, and color of the fruit, time of ripening, and soil requirements. At first the wild berries were harvested, but cultivation began about 1812, Capt. Henry Hall, of Barnstable (Cape Cod), being one of the earliest cultivators. The industry has now reached such proportions that there are several cranberry growers' associations, and a considerable body of periodical and book literature dealing with the subject. The plants are propagated chiefly by cuttings, and about three years

are required to secure the first crop after the cuttings are planted. This is one of the few "cultivated" crops that requires no cultivation; while fertilizer is not essential to a good yield, the crop may show a moderate average increase when fertilized, and this sub-

FIG. 486.—Harvesting cranberries with the Harrison scoop, Barnegat, N. J. (After Darrow. U. S. Dept. Agr.)

ject is being given attention by various growers and by some experiment stations. It has also been claimed that a larger yield is insured by keeping honey bees in the vicinity of the bog, thus insuring more extensive pollination. This, however, has not been definitely demonstrated. *Cf.* p. 397.

Like most cultivated crops, cranberries are more or less troubled with disease and pests. The principal disease is "scald," for which the best remedy appears to be bordeaux mixture, but on Cape Cod bogs this was found to cause severe injury to the roots. Numerous insects attack various parts of the plant, some of the commoner being the cranberry rootworm (*Rhabdopterus picipes*), the blackhead fire worm (*Rhopobota vacciniana*), the fruit worm (*Mineola vaccinii*), the tip worm (*Cecidomyia oxycoccana*), the blackhead cranberry worm (*Endemis vacciniana*), and others.

In earlier days the berries were picked by hand, but now practically all picking is done by forked scoops about sixteen inches wide, which act somewhat like a wooden rake pushed forward, the flat tines being so spaced as to catch the berries but allow the vines to slip through (Fig. 486). The average scoop will hold about six quarts when full, and scooping leaves the vines nicely raked out for trimming. The average yield is between 50 and 100 barrels per acre, but in rare cases the yield has risen to as much as 200 barrels. Machine picking has not proved entirely successful.

The fruit of the European cranberry (*Vaccinium Vitis-Idaea*) is also harvested as a crop, but this species is not cultivated. It is more highly prized in Europe than in the United States.[1] The plants are valued in shrubbery borders.

The order Ericales includes the following: White-alder Family (*Clethraceae*), including the Sweet Pepperbush (*Clethra*); Wintergreen Family (*Pyrolaceae*), including the Shin-leaf, Prince's-pine (Pipsissewa), and others; Indian-pipe Family (*Monotropaceae*), containing the saprophytes—Indian pipe (*Monotropa*), False Beech-drops, and Pine-drops; the Diapensia Family (*Diapensaceae*), with the Arctic and Alpine Diapensia (Fig. 487), the Pixie or Flowering Moss (*Pyxidanthera*) of pine barrens, and the southern *Galax* (Virginia to Georgia) whose large, shiny leaves are so much used in floral pieces.

ORDER, Primulales

The Primrose Order usually has one whorl of stamens opposite the petals, an unusual arrangement. Sometimes a second whorl

[1] The so-called "high-bush cranberry" is not a true cranberry, but an altogether different genus (*Viburnum Opulus*). Its fruit has slight economic value.

of staminodia occurs. The order has several characters in common with the Pink Order (Caryophyllales), namely, usually entire leaves, often mostly basal, a single-celled ovary with central placentation, and a double seed-coat.

The order includes the Leadwort Family (*Plumbaginaceae*), with *Plumbago, Limonium* (Sea Lavender or Marsh Rosemary),

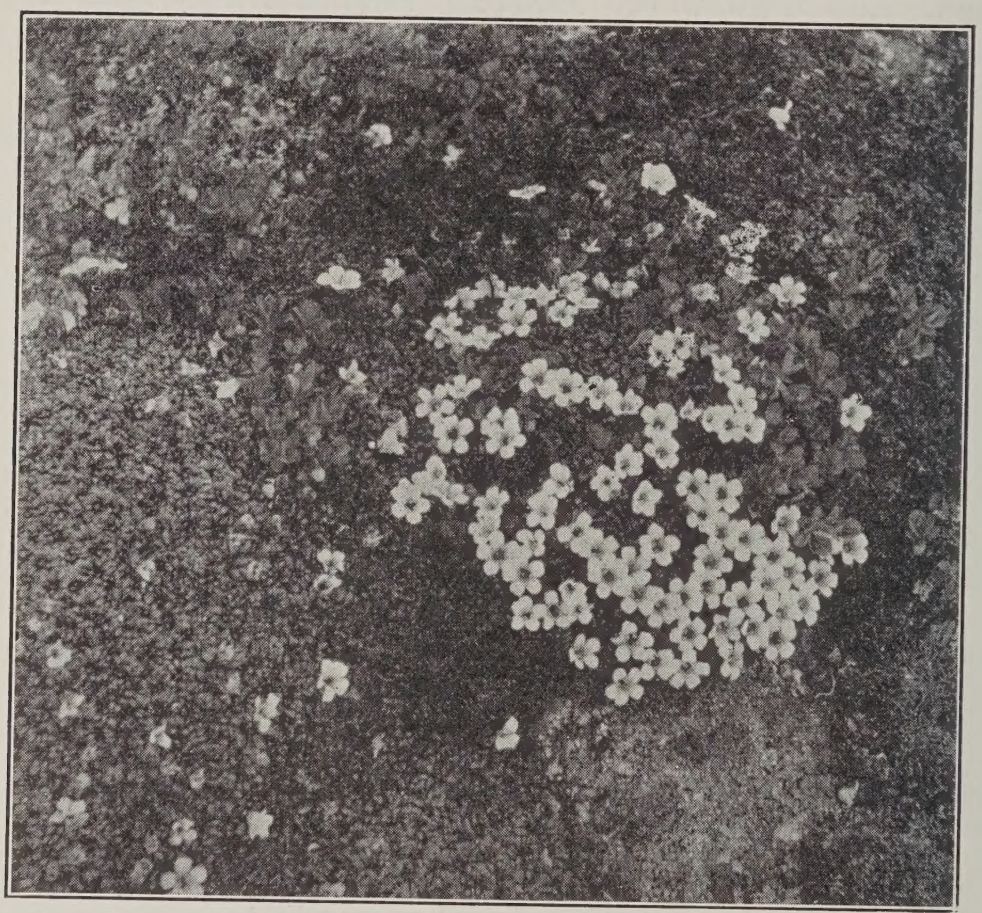


FIG. 487.—*Diapensia lapponica.* Photographed on the summit of Mt. Madison, New Hampshire, June 25, 1917, by Ralph E. Cleland.

the Primrose Family (*Primulaceae*), with the Primroses (*Primula*) (Fig. 488), Loosestrifes (*Lysimachia* and *Steironema*), American Cowslip or Shooting Star (*Dodecatheon*), and the Pimpernel (*Anagallis*), and a few other families.

ORDER, **Ebenales**

This order includes only shrubs and trees, chiefly tropical, with leathery, entire leaves, usually with two whorls of stamens, and large seeds. Here belong the Ebony Family (*Ebenaceae*), which

includes the Persimmon (*Diospyros*), the Sweet-leaf Family (*Symplocaceae*) with the Sweet-leaf (*Symplocos*), the Storax Family (*Styracaceae*), and the Sapodilla Family (*Sapotaceae*), which takes its name from the Sapote (*Casimiroa edulis*).

FIG. 488.—*Primula japonica*, growing in a Rock Garden.

SAPODILLA FAMILY

The most important economic plants of the Ebenales are probably the hundred or more species of the Sapotaceae Family which yield Gutta Percha. Chief of these are *Palaquium Gutta* (Fig. 489) and *Payena* sp. This gum is the best known non-conductor for heat and electricity. It resembles rubber, with which it is often, but erroneously, confused in the popular mind.

It is much less elastic than rubber, is very plastic when heated to 150° F., and, on cooling, retains whatever shape is given it when hot. All the species produce gutta percha in the same way, not in latex vessels or tubes, as in the case of Para rubber, but in numerous irregular intercellular cavities, which occur chiefly in the bark, and also in the leaves and pith, but not in the wood. The name gutta percha is derived from the Malay words, *getah* (sticky gum), and *pertia*. The latter word "is said to be the Malay name for one of the less valuable guttas and also for the Island of Sumatra. The term gutta percha, therefore, may be a corruption of the original native names, or merely mean Sumatra gutta."[1]

FIG. 489.—Gutta Percha plant (*Palaquium Gutta*). Flowering branch. (After Baillon.)

Most of the best gutta percha comes from a rectangular area extending about 6° north and south of the equator, and from 99°–119° east longitude. Other species yielding an inferior gum occur throughout the Malay Archipelago, in Indo-China, the Philippines, New Guinea, and northern South America. The trees, seldom exceeding 5–6 feet in circumference, do not form pure forests, but are mingled with other trees, and are seldom the most abundant. Recent observations show that the tree is of rapid growth, increasing as much as 1.5 inches or more per year. The tree attains a height of 70–100 feet, and produces 5000–10,000 seeds per year. It may also be reproduced from cuttings, layering, and by divisions at the base of the stem with roots attached.

Since gutta percha is practically unaltered by continued submergence in water it is the universal coating of submarine cables. It is also used in dental work, in electrical apparatus, and for

[1] Anon. Gutta Percha. British Empire Exhibition, London, 1924. Malayan Series No. XVIII. Freely drawn on for the above account.

funnels and bottles in the chemical laboratory where glass cannot be used.

The Sapodilla (*Achras Sapota*), of the Sapotaceae, bears an edible fruit with a yellowish and very sweet pulp. Its milky juice is one of the sources of *Chicle*, a gum-like substance which is the basis of chewing gum. Chicle is also obtained from the latex of the Bully-tree (*Mimusops globosa*) of the same family. It is more plastic than caoutchouc and more elastic than gutta-percha of which it is sometimes used as an adulterant.

STORAX FAMILY

The *Styracaceae* contain several ornamental shrubs and trees, valued for their white flowers, which are commonly fragrant and frequently pendulous in racemes. There are about 100 species, native in tropical and subtropical regions of Europe, Asia, and America. One of the hardiest northward is *Styrax japonica*, from China and Japan, commonly known as Storax. This grows as a shrub or tree, sometimes reaching a height of 30 ft., and bearing an abundance of pendulous white flowers which appear in June and July. A resin-like gum, the benzoin of the druggists, is obtained from *Styrax Benzoin* (of the Malay Archipelago) and not from the Spice Bush, *Benzoin aestivale*, which belongs to the Laurel Family.

Also in the Storax Family belongs the Silver Bell (*Halesia carolina*), named from Stephen Hales.[1] This large shrub or tree, with bright green leaves and drooping white flowers, is hardy as far north as Massachusetts.

EBONY FAMILY

The *Ebenaceae* are shrubs or trees, some species of which have a milky sap. Here belong the following well-known economic plants:

[1] Stephen Hales. (1677–1761), an early and noted student of plant physiology. Author of *Vegetable Statics*. Fellow of Corpus Christi college, Cambridge (England). He was a chemist and inventor as well as a botanist, and has been called "the true founder of the modern experimental method in physiology." Francis Darwin states that we must go back to Van Helmont (1577–1644) to find any one comparable to him as an experimentalist, and notes that, while "his successors have discovered much that was hidden from him," they have consciously or unconsciously, "all learned from him the true method and spirit of physiological work."

The common Persimmon or Date Plum (*Diospyros virginiana*), and the Japanese Persimmon (*D. Kaki*). The former may become a tree 50–100 feet high with flowers dioecious or polygamous, and the orange colored fruit a plum-like berry, 1–1½ inch in diameter, with 1–10 seeds, and the enlarged calyx at the

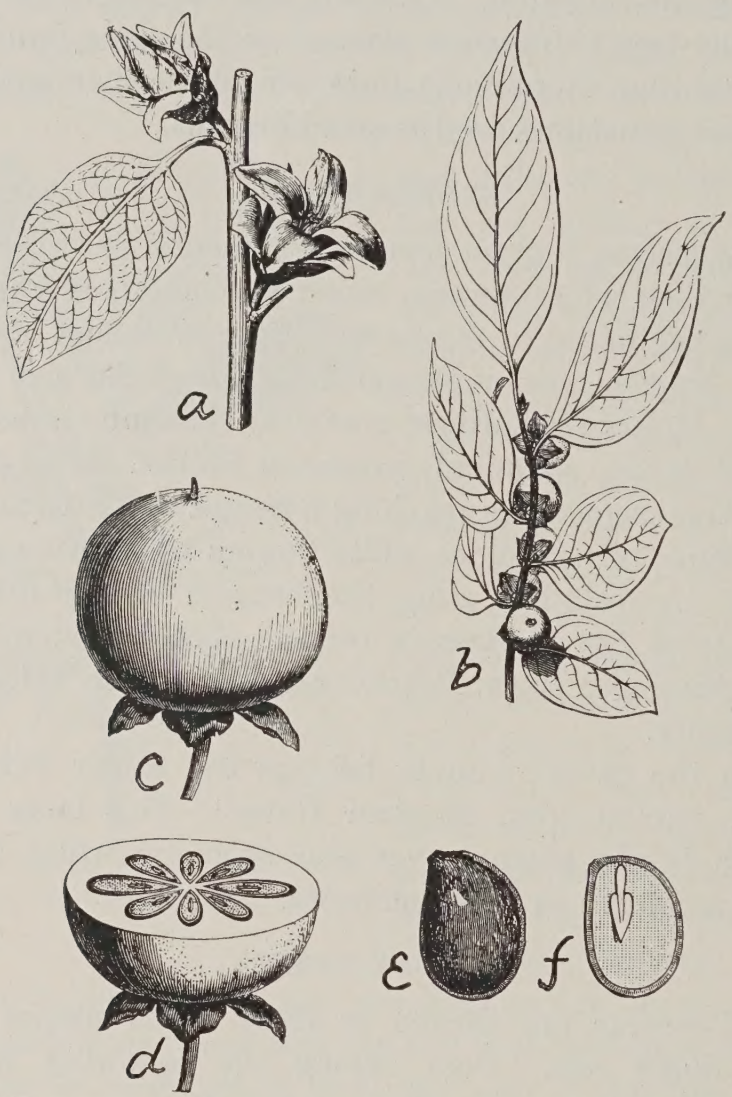


Fig. 490.—Persimmon (*Diospyros*). Branches with flowers and with fruit; fruit entire and in cross-section; seed entire and in longitudinal section. (After Baillon.)

base (Fig. 490). This species grows wild in most of the southern United States, and is hardy as far north as Rhode Island. There are 12–14 named varieties.

The Japanese persimmon or *Kaki* reaches a height of 40 feet, and bears a fruit 1½–3 inches in diameter, orange or reddish

colored, and roughly resembling a tomato. Some of the 18–20 varieties are more hardy than others, but few can stand zero weather, and the varieties do best in the United States in the cotton belt. The fruit is highly prized, especially in Japan. It ripens from August to November.

The green fruit is very astringent on account of the presence of soluble tannin, but this disappears during the process of ripening, which occurs between August 1 and December 1, depending on variety and locality. Contrary to an opinion held by some, frost is not necessary to ripening. Investigations by Lloyd indicate that, in ripening, the tannin (which is a colloid) is not destroyed, but unites with another insoluble substance of a gelatinous or cellulose-mucilage nature to form an insoluble tannin-colloid complex.[1] By this means the astringency of the unripe fruit disappears. The ripening may be accelerated by a method of "processing," which consists in subjecting the green fruit to the vapor of alcohol or of vinegar (a method used by the Arabs), or preferably by subjecting the fruit in a tightly sealed barrel to an atmosphere of carbon dioxide. By the Japanese method the carbon dioxide given off in the respiration of the fruit is utilized, but Lloyd[2] has described a method by which the process of ripening may be shortened to two days or less by exposing the green fruit to carbon dioxide at a gaseous pressure of 15 pounds.

Ebony is the wood of several species of trees of the same genus as the Persimmon. The ebony from India and Ceylon is from *Diospyros Ebenum*, native in those countries. Other species yielding ebony are *D. reticulata* (Mauritius), *D. melanoxylon* (East India), *D. tomentosa* (Bengal), *D. Montana* (India), *D. quaesita* (Ceylon), *D. Dendo* (Angola).

[1] This is similar to what takes place in the tanning of leather. The animal skin is impregnated with tannic acid or tannin, obtained from bark or other vegetable source, and the tannin unites with the mucilaginous fiber of the skin, by adsorption, rendering the skin tough and permanently pliable and imputrescible. If Lloyd's theory is correct, the method of ripening of the persimmon (and also of the date) is essentially a process of tanning.

[2] Lloyd, F. E. A practical method of artificially ripening Japanese persimmons. Proc. Ninth Ann. Meeting, Alabama Hort. Soc. 57–63. 1912. See also Science, N. S. **34**: 924–928. Dec. 29, 1911.

ORDER, Gentianales

The Gentianales comprise the Dogbane, Milkweed, Gentian, Logania, and Olive families. This and the following order have stamens inserted on the petals (*epipetalous*) and, with few exceptions, only two carpels.

OLIVE FAMILY

The most important family of the Gentianales is the Olive Family (*Oleaceae*), which includes the ash, olive, lilac, and privet. They are all shrubs or trees with opposite leaves, either simple or pinnately compound, calyx 4-cleft or rudimentary, corolla 4-cleft or with four petals, stamens usually two, and the ovary two-celled (Fig. 491).

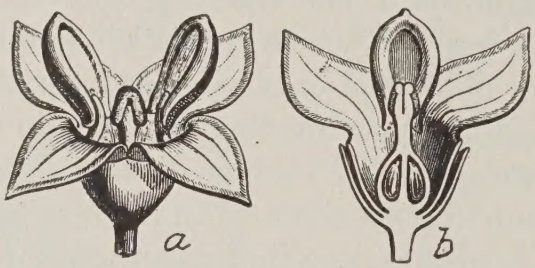


FIG. 491.—Olive (*Olea*). Flower entire and in longitudinal section. (After Baillon.)

The Ash (*Fraxinus*), with about 50 species, is an important timber tree.

THE OLIVE

The olives of commerce are the fruit of a small evergreen tree, *Olea europaea*. The wild species grows in most of the countries bordering the Mediterranean Sea, including France, Italy, Greece, Macedonia, Syria, Algeria, Morocco, and the Canary Islands. It is used as a stock on which cions of the numerous cultivated varieties are worked. Olives are also propagated by seeds (the seedlings being grafted), and by cuttings. The latter is the usual method in California. The tree has been cultivated from prehistoric times in Asia Minor. In foliage, inflorescence, and fruit the olive resembles the privet, except, of course, that the fruits (drupes) are larger and the flesh thicker in proportion to the pit or stone than in the privet (Fig. 494).

The green olives of the markets are the unripe fruits, while the dark purple olives are the ripe fruits.

It is difficult to get the seeds to germinate, and they are usually either soaked in a solution of caustic soda to soften the pit, or the apex of the pit is clipped off by a simple apparatus. Soaked seeds may not germinate for a year, but clipped seeds sprout within a few weeks.

The olive is subject to a serious disease, "olive-knot," caused by a bacterium (*Bacterium savastanoi*), which produces knot-like swellings or tumors. The disease is infectious. There are also less serious fungous diseases of the leaves and roots. The fruits contain a bitter principle which is removed by soaking them in potash or soda lye. This softens the pulp which is then artificially hardened and the olives are preserved and marketed in brine.

Olives are also important as the source of olive oil, which is extracted by crushing and then pressing the fruits or, more recently, by subjecting the fruits, in containers, to diminished air pressure, as a result of which, the oil exudes from the pulp.

THE LILAC

The lilac (*Syringa*), introduced into Europe in the 16th century by way of Constantinople, is cultivated in several hundred horticultural varieties for the beauty of its inflorescence. The older botanists (*e.g.*, Gerarde, in his *Herball*, 1597) included both the lilacs and the mock orange in the genus *Syringa*.[1] Later Tournefort (1700) restricted the name *Syringa* to designate the mock orange, placing the lilac in the genus *Lilac*, but subsequently Linnaeus adopted *Syringa* for the lilac, referring the mock orange to the genus *Philadelphus*, named (by Caspar Bauhin) from the

[1] In the second edition of Gerarde's *Herball*, Chapter 61 (p. 1399) is entitled "Of the white and blew Pipe-Privet," and he describes and figures, 1. *Syringa alba*, White Pipe, and 2. *Syringa caerulea*, Blew Pipe. The former is the mock orange, the latter the lilac. Note the use of binomials more than 150 years before Linnaeus. (*Cf.* foot-note, p. 563.)

As to the names, Gerarde says (p. 1401): "The later Physitians call the first *Syringa*, or rather σύριγξ: that is to say, a Pipe, because the stalks and branches thereof, when the pith is taken out, are hollow like a pipe: it is also many times syrnamed *Candida*, or white, or *Syringa candida flore*, or Pipe with a white floure, because it should differ from *Lilach*, which is sometimes named *Syringa caerulea*, or blew Pipe."

Egyptian king Ptolemy Philadelphus. Botanists have followed the usage of Linnaeus, but in common English speech Tournefort's name Syringa has, unfortunately, persisted for the mock orange.

Fig. 492.—Lilac (*Syringa vulgaris*, var. Vestale). Young fruit cluster.

With the exception of *Syringa sempervirens*, lilacs are deciduous shrubs or small trees, with opposite, exstipulate, and usually entire leaves. Rarely the leaves are pinnatifid (*e.g.*, *S. persica* var. *laciniata*), or pinnately compound (*e.g.*, *S. pinnatifolia*). The flowers, in panicles, have a small bell-shaped (*campanulate*) calyx with four teeth, a salverform corolla with a cylindrical tube with four limbs, two stamens, and an ovary with two locules. The fruit (Fig. 492), is a leathery capsule, dehiscent at the locules, each of which contains two seeds. The fruit of *S. sempervirens* resembles a fleshy drupe, having only one seed. There are 25–30 species ranging from south-eastern Europe to the Himalayas, and from Japan to northeastern Asia.

Some forms are strongly and sweetly scented, others only slightly or not at all so, while *S. amurensis* and others have an odor that closely resembles their relative the privet. *Syringa japonica* may become a real tree, reaching a height of about 30 feet while *S. vuzgaris* and two or three other forms may become tree-like with a height of 10–20 feet.

THE PRIVET

The Privet (*Ligustrum*), one of the most successful, and therefore one of the commonest hedge plants in the east, and, in fact, in nearly all parts of the United States, has become naturalized as an escape from cultivation, from Maine to Ontario, and south to North Carolina. The opposite, exstipulate leaves have short petioles and entire margins, and the perfect flowers are in terminal

FIG. 493.—Privet (*Ligustrum ovalifolium*). Inflorescence. Note the similarity to the well-known inflorescence of its relative, the Lilac.

panicles (Fig. 493), much resembling the inflorescence of its near relative the lilac, although very much smaller. The bell shaped calyx is obscurely four-toothed, and the funnel shaped corolla has a short tube with four spreading lobes. There are two stamens, and the fruit is a 1–4-seeded berry-like drupe, strikingly suggesting small ripe olives (Fig. 494). There are approximately 50 species, most of which are native in the Himalaya Mts. and

eastern Asia. One species is indigenous in North Africa, one in Europe, and one extends south to Australia.

Some species are evergreen, others deciduous. Of the deciduous species the most common in the eastern United States are the California privet (*Ligustrum ovalifolium*), the Ibota privet (*L. Ibota*), and the European privet (*L. vulgare*), also some-

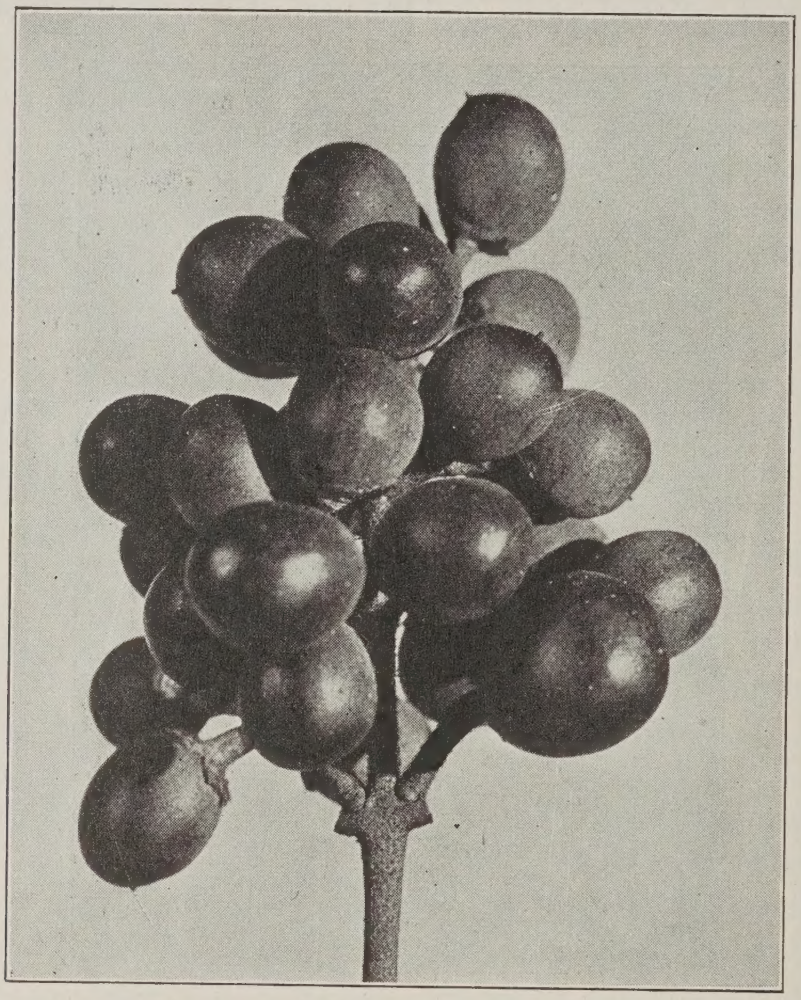


FIG. 494.—Ibota privet (*Ligustrum Ibota*). Cluster of fruit. Note the similarity of the fruit to that of its relative, the olive. Enlarged about 5 times.

times called "prim." The California privet, introduced from Japan, has several varieties, as, for example: *multiflorum*, more freely flowering than the type; *tricolor*, leaves variegated with white and yellow; *variegatum*, leaves green variegated with yellow; and *aureo-marginatum*, green leaves with yellow edges. Bud sports of one or the other of these varieties often appear on plants of the original green-leaved species. Similar variations,

with the same names, also appear in *L. vulgare*. This species, (together with *L. Japonicum*, and *L. sinense*) are among the best known of the evergreen forms.

When not clipped, the various species may attain the stature and habit of trees. The plant is very easily propagated by seeds and by hardwood and (in summer) greenwood cuttings. In fact, in some nurseries the plant is propagated by chopping up branches in a stalk-cutter and sowing them in furrows, as is also done with sugar-cane and stolons of Creeping Bent grass (*Agrostis stolonifera*).

FORSYTHIA

The Golden-bell (*Forsythia*) is one of the earliest and also one of the most beautiful of spring flowering shrubs. It is named from William Forsyth (1737–1804), formerly director of the Royal Garden at Kensington, England, and should therefore be pronounced with a long "y." The deciduous leaves are opposite, with entire or serrate margins; they vary (as in lilac) from simple to compound with three leaflets. The flowers, appearing before the leaves, have a deeply four-lobed calyx and corolla, the lobes of the corolla (commonly called petals) being much longer than the corolla-tube, in contrast to lilac and privet. There are two stamens, and the fruit is a 2-celled dehiscent capsule. There are four species (*F. suspensa*, *F. intermedia*, *F. viridissima*, and *F. europaea*), indigenous to Japan, China, and Southeastern Europe. *F. intermedia* is a cross between *F. suspensa* and *F. viridissima*. There are about ten varieties or horticultural forms of these species. They are propagated by cuttings of both green and hardwood, and also by seeds. The tips of the pendulous branches often take root where they touch the soil, producing numerous shoots.

ORDER, Polemoniales

The Polemoniales are mostly herbs and twining vines, with a few shrubs and trees (*e.g.*, *Catalpa* and *Paulownia*).

MORNING-GLORY FAMILY

The Morning-glory Family (*Convolvulaceae*) has about 40 genera and 900 widely distributed species of herbs, vines, shrubs, and trees, including Morning-glories proper (*Ipomoea* sp.), the

troublesome, weedy Bindweed (*Convolvulus*) (Fig. 495), the parasitic Dodders (*Cuscuta* sp.), the wild and cultivated Phloxes, Sweet William, and the Sweet Potato (*Ipomoea Batatas*).

THE SWEET POTATO

The sweet potato is economically the most important plant of this family. Evidence points to tropical America as its place of origin. It is said that models of the sweet potato have been found in prehistoric graves in Peru, closely resembling some of

FIG. 495.—Bindweed (*Convolvulus arvensis*).

our modern varieties. Between the Atlantic ocean and the Rocky Mountain Plateau the crop is not grown north of about the latitude of central New Jersey. It is extensively grown in southern California under irrigation.

The flower has five sepals and a sympetalous, bell-shaped corolla (*Cf.* Fig. 495); the five stamens are inserted on the tube of the corolla. The base of the ovary is surrounded by a disk, and the style bears two stigmatic lobes. The ovary appears to have four cells, each containing one seed; morphologically, however, as

its developmental history shows, the ovary has two cells, each with two seeds, but these are divided by a so-called "false" wall or partition, as is commonly the case in the Convolvulaceae.

Being a warm-climate plant its cultivation is largely confined to regions having a mean summer temperature of not less than 72° F., and a growing season of at least 175 days. The plant blooms only rarely in the north. Many growers in the northern range of

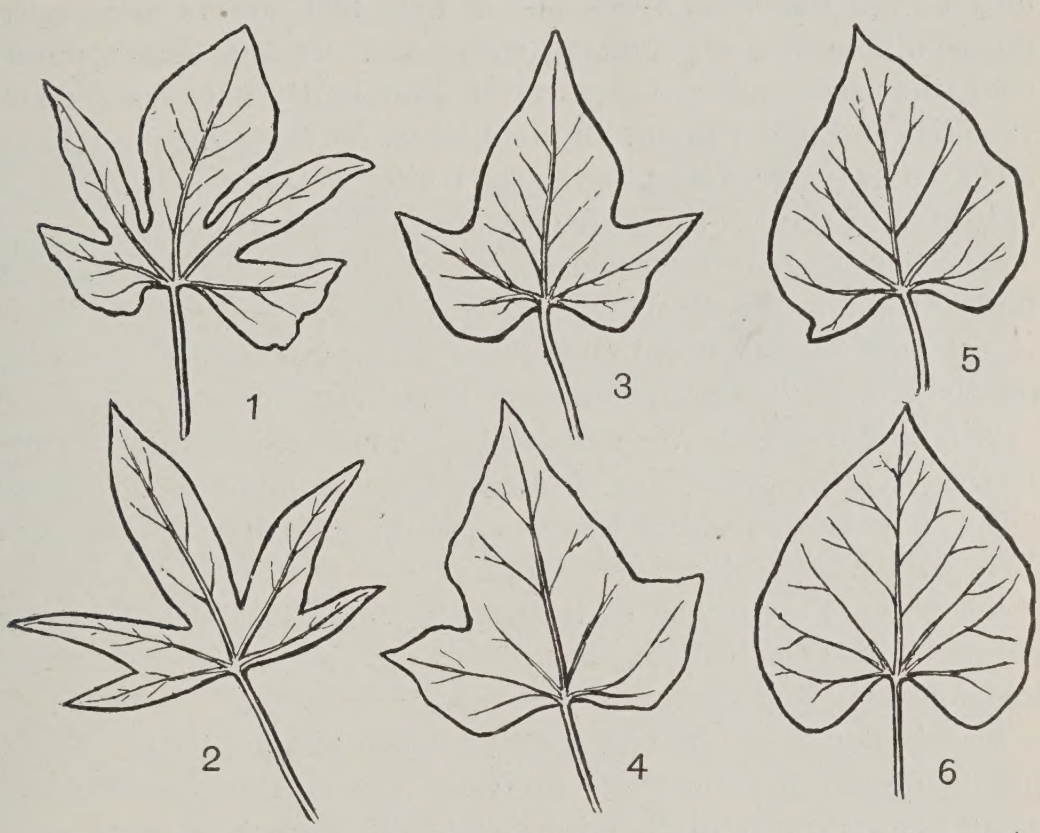


FIG. 496.—Sweet Potato (*Ipomoea Batatas*). Typical leaf-forms characteristic of three classes of varieties, namely: cut-leaved, shouldered, and entire. The varieties are: 1, Sugar or Creole; 2, Java; 3, Strasburg; 4, Bermuda (Red Bermuda); 5, Big Stem Jersey; 6, Pumpkin. (Redrawn from F. H. Burnette. Louisiana State Agr. Exp. Sta.)

its cultivation have never seen a blossom, though in the tropics most of the varieties flower freely. The species appears to be what Garner and Allard have called a "short-day" plant—one in which the short day of lower latitudes favors flowering and intense tuberization, while the longer day of higher latitudes favors non-flowering, greater development of fibrous roots, and limited tuberization. This was shown by Garner and Allard to be the case with the true yam, *Dioscorea alata*, (*Cf.* pp. 268–270).

Still, even where flowers are freely produced, the plants seldom form fruit and seeds, even when artificial self-pollination has been practised.[1]

Stamens and pistils mature at the same time (as in all self-pollinated species), but it is not easy to secure the formation of seeds by either self- or cross-pollination. Some varieties appear to cross more readily than others. In 1894 Burnette[2] obtained only eleven imperfect seeds out of over 800 flowers artificially cross-pollinated and protected with bags. It is probable, however, that seeds are produced more abundantly between certain varieties and under favorable conditions, for there are more than 50 varieties under cultivation in the United States alone, although only about twelve of these are commercially important.

The varieties are classified chiefly on the basis of leaf-characters, as follows (Fig. 496):

1. Those having deeply cut foliage, *e.g.*, Barbadoes, Georgia, Southern or Yellow Yam,[3] Vineless, Bunch, and others.

2. Those having leaves more or less shouldered, *e.g.*, Bermuda, Early Golden, Java No. 3, Peabody, Triumph, and others.

3. Those having entire leaves, *e.g.*, Big Stem Jersey, Pumpkin Yam, Delaware, California, and others.

These varieties differ in their time of maturing, and in the character of their "tubers," some being dry and mealy, and others moist fleshed; some yellow, others red.

Sweet potatoes are propagated vegetatively, either from plants produced from roots or from vine cuttings. When an early truck crop is desired they are started in coldframes, and where the growing season is too short for cold-frames to serve,

[1] Stout, A. B. The flowers and seed of sweet potatoes. Jour. New York Bot. Gard. **25**: 153–168. June, 1924.

[2] Burnette, F. H. Sweet potatoes. Bull. State Exp. Sta. Baton Rouge, Louisiana. Second Ser. 30. 1894. For a different classification see Thompson, H. C. and James H. Beattie. Group classification and varietal descriptions of American varieties of sweet potatoes. U. S. Dept. Agr. Bull. No. 1021. April 17, 1922.

[3] The name *yam* is properly applied to the fleshy tuber of various species of Dioscorea (see p. 893). This name (*nyam*), known to the negroes in Africa as designating *Dioscorea*, was probably applied by them to the sweet-potato as being the American plant that most closely resembled the *Dioscorea*.

they are started in hotbeds with bottom heat produced by fresh manure or even by flues connected with a furnace or stove.

Structure and Morphology of the "Tubers."—The edible portion of the sweet potato is not, botanically speaking, a tuber, but a fleshy root (Fig. 497). Its shape varies from fusiform, to napiform or irregular-spherical, depending upon the variety

FIG. 497.—Sweet Potato (*Ipomoea Batatas*). Field in harvest time. After plowing, the sweet potatoes are raked out by hand and allowed to dry before being placed in barrels or baskets. (U. S. Dept. Agr. Farmers Bull. No. 1267).

(Fig. 498). In some varieties the skin is smooth, in others irregularly ribbed. Secondary roots grow out from the fleshy root in vertical rows, each rootlet surrounded by a depression somewhat like the "eye" of a potato. The formation and activity of primary and secondary cambium result in giving the so-called "tuber" an unusual structure for dicotyledonous roots, but the fact that the protoxylem strands are next to the

pericycle and develop toward the center, as is typical for roots, indicates that the "tuber" is, morphologically, a root.[1]

The Physiology of Tuber-ripening or Maturing.—During the growth of the sweet potato plant the roots, of course, are taking in water and distributing it to the plant. As is always the case in normal healthy plants, the extent of the root-system is adjusted to the water-need of the plant, and this, in turn, depends upon the rate of transpiration from leaves and stems. During this same time, also, the green leaves are, by photosynthesis, manufacturing carbohydrate material which, in the form of sugar

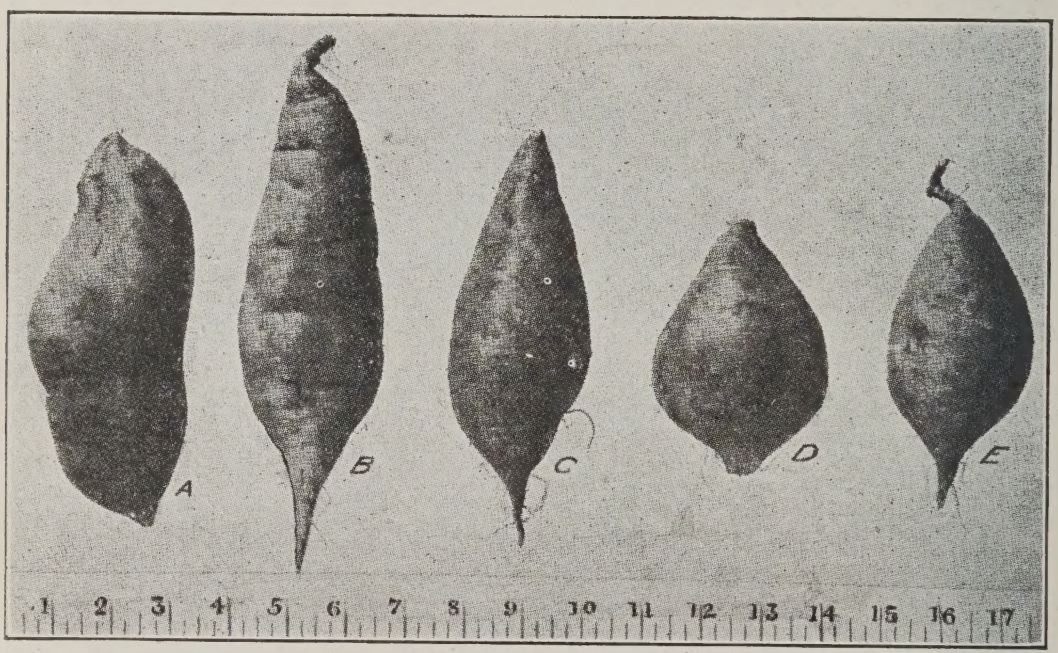


FIG. 498.—Sweet Potatoes (*Ipomoea batatas*). Shapes of the root-tubers of four dry-fleshed varieties. A, Big-Stem Jersey; B, Triumph; C, Yellow-Jersey; D, Yellow Jersey; E, Red Jersey. Note the two distinct types of the Yellow Jersey variety. (After F. E. Miller. U. S. Dept. Agr.)

dissolved in the sap, is distributed to all feeding parts of the plant, but the greater part of its passes into the tubers, where much of it is converted into starch for storage. What happens now, toward the end of the season, when the vines begin to die? In the first place photosynthesis and transpiration begin to diminish until they cease altogether with the death of all the vines. While the vines are dying, much, if not all, of the dissolved photosynthate passes into the root-tubers where it is converted into starch.

[1] Artschwager, Ernst. On the anatomy of the sweet potato root, etc. Jour. Agr. Res. **27**: 157–166. Jan. 19, 1924.

With the death of the vines transpiration also ceases, but the roots continue to take in water from the soil and deliver it to the tubers. This continuation of intake of water, after transpiration has ceased, results in the accumulation of an excess of water in the tubers, tending to make them "watery." As Hasselbring[1] has pointed out, a knowledge of these facts may be useful as an aid in determining the time for harvesting the crop; for it is evident that, if marked changes occur in the roots during the latter part of the season, the time of harvest will depend upon the purpose for which they are destined, whether for storage, stock feed, silage, or the manufacture of starch. In the last case it is evident that the crop should be harvested when the starch content is greatest. This is during the latter part of the period of growth, when the composition of the roots remains notably uniform, with high percentage of starch and low percentage of sugar.

So long as the vines continue active the carbohydrate content of the attached roots remains practically unchanged, and the roots cannot, therefore, be said to undergo a definite process of ripening, in the sense of a progressive transformation of one reserve substance into another, such as the change of starch into cane sugar and invert sugar during the ripening of apples.

Hasselbring and Hawkins[2] made a study of the carbohydrate transformations that occur in sweet potatoes during storage. These changes, which do not begin until materials cease to flow into the tubers from the vines, consist in the transformation of starch into cane sugar (chiefly) and reducing sugars (Fig. 499). This change continues from about October to March. The reducing sugars furnish the chief material for respiration, and therefore gradually diminish in amount. From March until June, as the temperature rises, the cane sugar is largely re-transformed into starch. Since these changes are not begun while the plant is still growing, the potatoes may be safely kept in the ground until the vines are injured by frost.

[1] Hasselbring, Heinrich. Behavior of sweet potatoes in the ground. Jour. Agr. Res. **12**: 9–17. Jan. 7, 1918. I have freely followed Hasselbring's phraseology after the above citation.

[2] Hasselbring, H. and L. A. Hawkins. Physiological changes in sweet potatoes during storage. Jour. Agr. Res. **3**: 331–342. 1915. The phraseology of these authors is also closely followed without quotes.

The excessive accumulation of water is more detrimental to successful storage than any other one factor, since it renders them more liable to injury by decay than when the water content is normal. The roots should, therefore, not be left long in the ground after the death of the vines. To reduce this excess of water is the object of the process of curing.

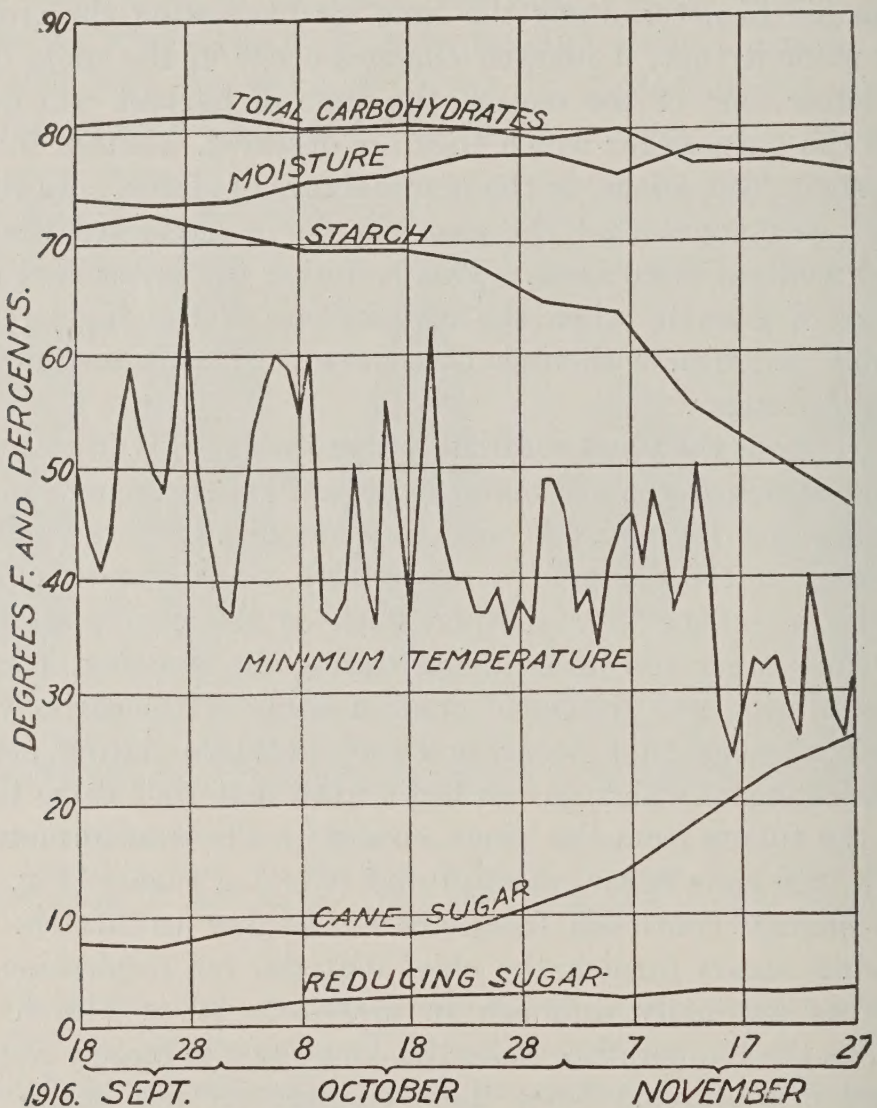


FIG. 499.—Sweet Potatoes. Chart showing changes in composition of the tubers of the Big Stem variety during the latter part of the season; also the minimum temperature at the U. S. Weather Bureau Observatory at Washington, D. C., some 20 miles distant, during that period. The ordinates indicate percentages in the one case and degrees Fahrenheit in the other. (After Hasselbring.)

MINT FAMILY

The Mint Family (*Labiatae*) contains about 160 genera and 3000 species, mostly herbs, but some shrubs. The herbaceous

species are characterized by stems that are generally square in cross-section, bearing opposite leaves that are aromatic from the presence of small glands with which the leaves are dotted (*punctate*). These glands contain a volatile oil, characteristic for the species. The irregular flowers are characterized by a highly modified corolla having two lips or *labia* (singular, *labium*),

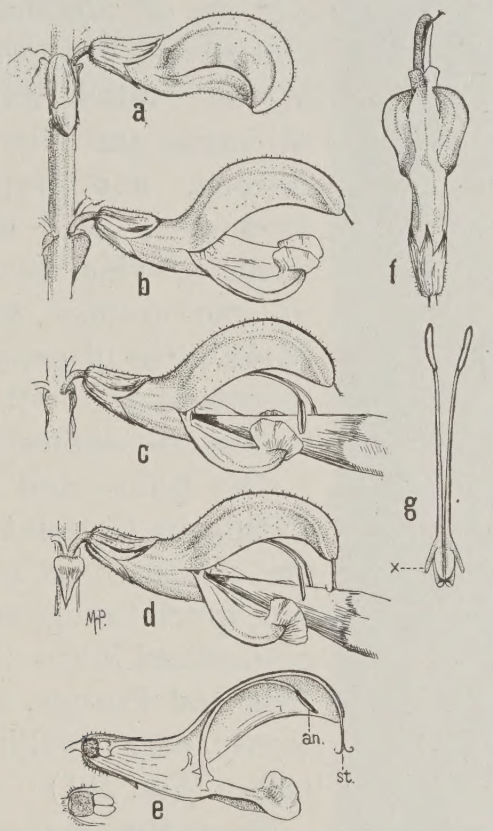


FIG. 500.—*Salvia sp.* (One of the Labiatae). *a*, flower bud; *b–f*, various views of the open flower; *an.*, anther; *st.*, stigma; *x*, projections near the base of the filaments. The lead pencil is made to imitate an insect visiting the flower for pollen. By pressure at the base of the filaments, the anthers are brought into contact with the surface of the pencil, which thus becomes covered with pollen. When the next flower is visited the stigma, having then bent down and spread apart, receives the pollen from the other flower. Thus is accomplished cross-pollination. In *b*, before the visit of the insect, the stigmatic surfaces are still in contact, so that pollination is not possible.

whence the family name. The upper lip results from the fusion of two petals, the lower lip by the fusion of three. The stamens are in two pairs of unequal length (*didynamous*), or only two (Fig. 500). The superior ovary is 4-lobed or parted, and the fruit contains four one-seeded nutlets or achenes. In the mints the stamens usually shed their pollen before the stigma is receptive, *i.e.*, the flowers are *proterandrous*.

The Labiate genus *Mentha* contains the Peppermint (*M. piperita*) and Spearmint (*M. spicata*), both naturalized in the United States from Europe. These are perennial herbs, propagating freely by rhizomes or runners, and often crowding out other plants. They are both cultivated, and supply a powdered drug and an oil distilled from the stems and leaves. Peppermint is cultivated in the United States (especially in Michigan and New York), England, Europe, and Japan. The Japan product is used chiefly in making menthol, which is also derived from *Mentha arvensis* and *Mentha anarvensis*. Oil of peppermint and oil of spearmint are both extensively used in flavoring confections.

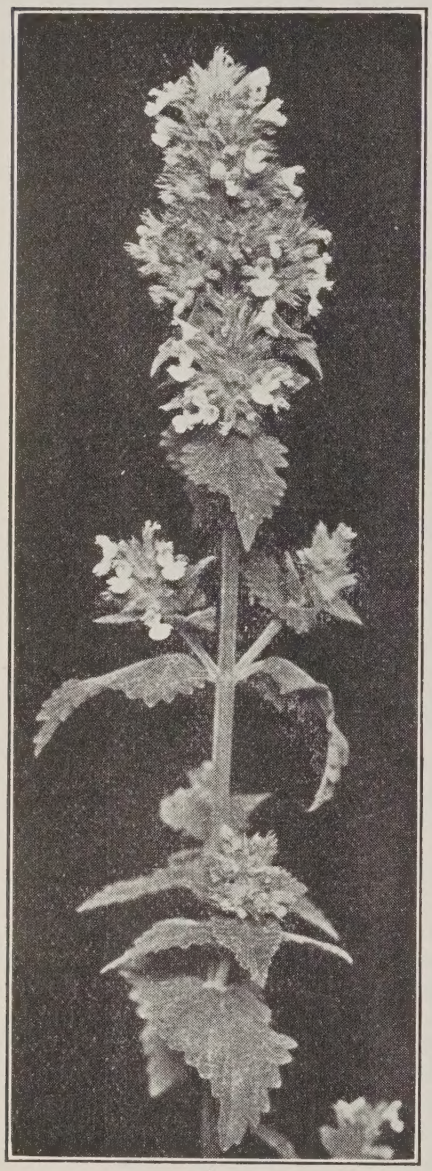


Fig. 501.—Catnip (*Nepeta Cataria*).

The leaves and flowering tops of Catnip or Catmint (*Nepeta Cataria*) are also used as a drug. This is a tall, much-branching, perennial herb, naturalized in the United States from Asia and Europe, and growing commonly near dwellings and in waste places (Fig. 501).

One of the commonest Labiate weeds is the Self-heal or Heal-all (*Prunella*, or *Brunella, vulgaris*), adventive from Europe, and common in fields and woods throughout North America. The flowers grow three in a cluster in dense bracted heads or spikes. The seeds of this plant are often found as adulterants with clover seed.

The Sage (*Salvia*) has about 500 species, of which some 30 or more are found in North America. *Salvia officinalis*, as its name denotes, is officinal. *Salvia splendens*, the Scarlet Sage or common "salvia," with calyx and corolla both scarlet, is one of the most showy of late summer and fall flowers; it has over

15 horticultural varieties. *Salvia azurea grandiflora*, with showy blue corolla and bluish calyx, flowers in August. *Salvia Sclarea*, flowering in June, is a strikingly beautiful plant with its deep pink colored bracts and calyx, and its pink-white corolla. It is often called "clary."

Other labiates of economic importance are the following, cultivated as condiments: Thyme (*Thymus vulgaris*), Sweet Marjoram (*Origanum Majorana*), Sweet Basil (*Ocimum Basilicum*), Summer Savory (*Satureia hortensis*).

CHAPTER XXIV

SYMPETALOUS DICOTYLEDONS (CONTINUED)

ORDER, Polemoniales (Concluded)

POTATO FAMILY

No family of the Polemoniales is as important, economically, as the Potato Family (*Solanaceae*), containing the potato, tomato, egg-plant, tobacco, henbane, belladonna, and Jimson-weed. Of the 1500–1600 species in the family only about six bear tubers. This and the following family (Figworts) have a two-celled ovary with numerous seeds, but the Potato Family has regular flowers and five stamens, while the Figwort Family has a more or less irregular corolla with four (often 2, rarely 5) stamens in two groups (*didynamous*).

THE TOMATO

The tomato (*Lycopersicum esculentum*) is, as everyone knows, cultivated for its fruit. The genus comprises four or more species, natives of South America. The calyx and corolla are five- (rarely six-) parted, the 5 or 6 stamens are inserted on the throat of the corolla, the ovary is 2–3 celled, the style simple, and the calyx persistent in the fruit (Fig. 502). The cultivated tomato was not known in Europe until after the discovery of America. In his *Historiae Plantarum* (1651, Liber XXXIV, p. 621), Bauhin, under the caption *Mala aurea odore foetido quibusdam Lycopersion*, refers to the plant by the common name *Tumatle Americanorum*, and this is one of the earliest occurrences of the word which has finally come down to us as *tomato*. Bauhin also gives, as one of its numerous names, *Mala Peruviana*, and this name, together with other evidence, points to Peru as the country from which the earliest specimens were received.

One of the earliest illustrations of the plant is that by Dodoens (*Cruydt-Boeck*, Antwerp, 1644, p. 750), reproduced here as Fig.

503. Dodoens calls it Gulden-Appelen. They were at one time commonly known as Love Apples. The various horticultural varieties have a tendency to escape from cultivation and run wild. The "cherry-tomato" has been found wild in Peru,

FIG. 502.—Portion of a tomato plant, showing leaves, flowers, and fruit.

Mexico, and the southwestern United States. Within the past sixty years the fruit has been considered, in certain localities, as not edible, and there was a widespread belief that it was liable, if eaten, to cause cancer and other ills. As late as the early and middle nineteenth century it was commonly known in the

FIG. 503.—Tomatoes or Gulden-Appelen. Reproduction of one of the earliest known illustrations. (After Dodoens, *Cruydt-Boeck*, Ed. 1644, p. 750.)

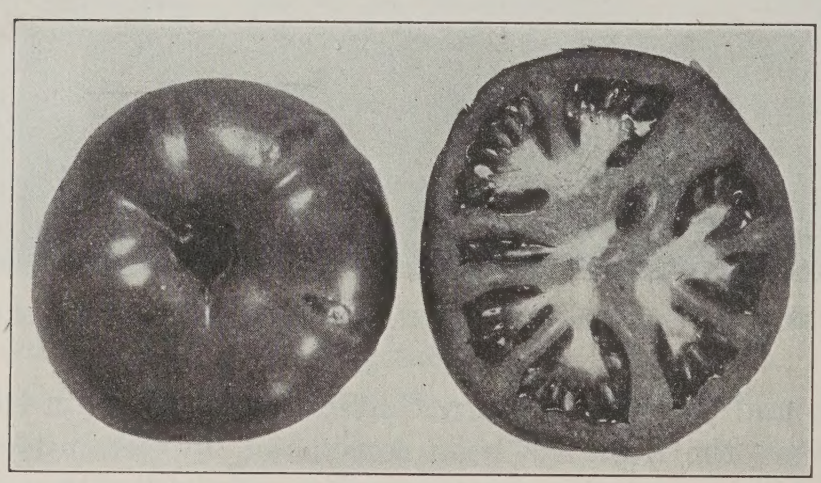


FIG. 504.—Fruit of the tomato (*Lycopersicum esculentum*). A berry, showing seeds (ripened ovules) attached to the placentas, and inclosed in the tissue of the ripened ovary.

eastern United States as "love-apple," and was cultivated only for ornament.

Since it has been recognized as edible, the fruit (Fig. 504) has been greatly improved by breeding, the improvement consisting in increased size, a more solid-meated fruit, and especially in increased smoothness of surface, the earlier varieties being very angular or lobed. The tomato has 500–600 varietal names in the catalogs of American seedsmen, and many additional names in foreign countries. These horticultural forms have been produced by crossing various wild and cultivated types. The currant, cherry, pear, husk, and other forms are now grown chiefly for curiosity or ornament. An Australian variety, known as Harrison's Prolific, is reported[1] to have grown "in 12 months to a height of 11 feet, attained a spread of 16 feet, and produced 100 dozen fair sized fruits."

One of the early successful forms, the Trophy, first came on the market about 1870. Single seeds cost 25 cents each, or Five Dollars for a packet of 20 seeds. The Italians appear to have been the first to use the tomato for food, being followed by the French, then by the English. Commercial canning began in 1847.

The Cherry Tomato (*L. cerasiforme*), Pear Tomato (*L. pyriforme*), and Currant Tomato (*L. pimpinellifolium*) are of slight horticultural importance.

Related genera include the Musk Tomato (*Physalis pubescens*), the tropical Tree Tomato (*Cyphomandra betacea*), and the Red Peppers (*Capsicum annuum*). The latter are the source of Cayenne pepper, and are used in the manufacture of Tabasco sauce and "ginger" ale. There are numerous other culinary and officinal uses.

From recent studies D. F. Jones[2] has concluded that the dry pollen of the tomato adapts itself for wind-pollination, and found little evidence of pollination by insects. While close-pollination seems to be the rule, the best results are obtained when a flower is pollinated by pollen from another flower on the same plant, rather than by its own pollen. The fruit often sets without pollination (*parthenocarpy*).

[1] U. S. Dept. Agr. Bur. Plant Ind. Inventory of Seeds and Plants Imported by the Office of Foreign Seed and Plant Introduction during the period from January 1 to March 31, 1921. Washington, 1923.

[2] Jones, D. F. *Natural cross-pollination in the tomato.* Science. **43:** 509–510. April 7, 1916.

Studies of Sando[1] show that, during the ripening period of the tomato, there is an increase in moisture, acids, and sugars and a decrease in solids. Sugars increase from 25.66% in fruit 14 days old to 48.32% in ripe fruit. Starch, at the same time, decreases from 15.84 to 2.65%, the most marked decrease taking place while the color is changing from green to red.

FIG. 505.—Potato (*Solanum tuberosum*). Portion of branch bearing flowers. *Cf.* Fig. 508. (Photo by E. M. Kittredge.)

When tomatoes are picked green for shipment they have a flavor, when ripened, greatly inferior to fruit ripened on the vine. Sando found that the effect of poor ventilation during ripening was to increase the acid content of the fruit about 138% over that of vine-ripened fruit. He concludes that "the combined results of picking fruit green, of wrapping it, and of closing the cars in transit probably account for the total differences existing in quality between commercially shipped and vine-ripened tomatoes."

THE POTATO

The genus *Solanum* contains herbs, shrubs, vines, and trees. Fruticose (*i.e.*, shrublike) and arboreal species of *Solanum* are common in equatorial South America, while, in the hummocks and pinelands of Florida, *Solanum verbascifolium* ranges from a shrub to a small tree, and is locally known as the "Tree Potato" or "Potato-tree." The flowers of *Solanum*, with parts in fives, are in racemes, panicles, umbels, or cymes (Fig. 505), the corolla is valvate or imbricate in the bud, and the fruit is a 2–5 celled

[1] Sando, Charles E. *The process of ripening in the tomato*, etc. U. S. U. S. Dept. Agr. Bull. 859. 1920.

berry or capsule, with many seeds (Fig. 506). The stamens are inserted on the corolla, and the calyx persists in the fruit (Fig. 507).

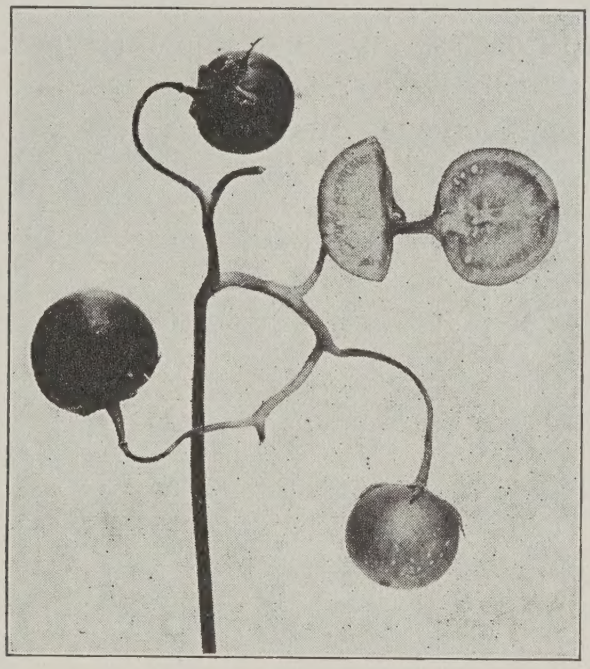


FIG. 506.—Potato Fruit or "balls," natural size. (After H. W. Mumford Univ. of Illinois Agr. Exp. Sta.)

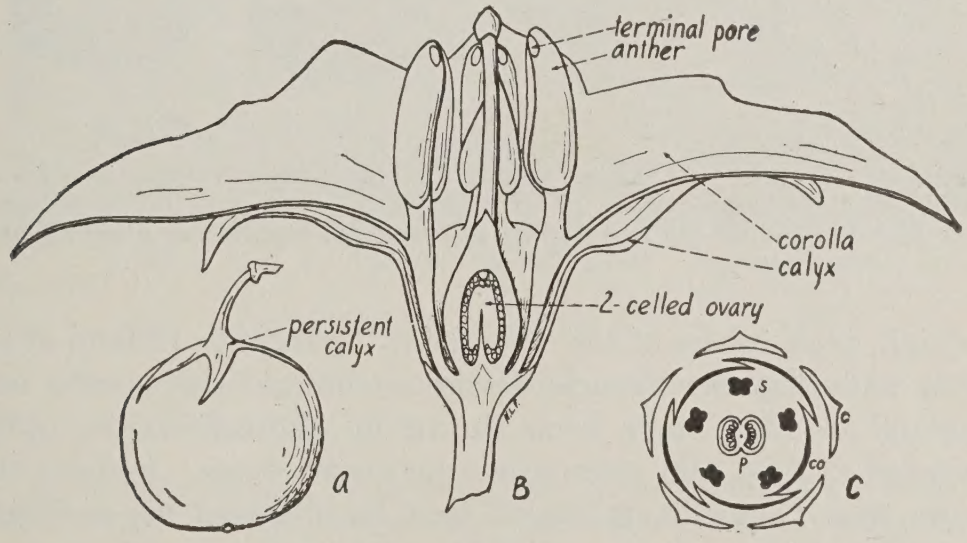


FIG. 507.—Potato (*Solanum tuberosum*). *A*, fruit; *B*, flower in median longitudinal section; C, ground-plan of the flower. (After Robbins.)

The potato (*Solanum tuberosum* L.) was found in cultivation from Chile to New Granada (Colombia) when the Spanish explor-

ers first reached the new world. It was not, however, known on the east coast of South America, though another species, *Solanum Commersonii*, of no economic value, grows wild in southern Brazil and in Uruguay and adjacent parts of Argentina.

According to Roze,[1] the first mention of the potato in literature appears to be that by Pedro de Ceica de Leon, in his *Chronica del Peru*, 1553. That Thomas Herriot, a companion of Sir Walter

FIG. 508.—Potato. At the left a flowering branch; at the right, underground portion of stem bearing roots and stolons with tubers, and tubers enlarged. Note that the stolons are represented as branched, a character rarely, if ever, seen in modern potatoes. (From Gerard's *Herball*. Ed. 1633, p. 927.)

Raleigh, took tubers of the "Virginian" potato to Ireland about 1585, and that Sir Francis Drake introduced the potato into England in 1586, have been shown by Safford[2] to be myths invented at least 100 years after the above dates. Safford also shows that Gerard's statement that he obtained his specimen "from Virginia, otherwise called Norumbega," cannot be correct. The potato was introduced into Europe from South America by

[1] Roze, Ernest. Historie de la pomme de terre traitée aux points de vue historique, cultural et utilitaire. Paris, 1898.

[2] Safford, W. E. Jour. Heredity. **16**: 113–126, 175–184, 217–230. 1925.

Spanish explorers soon after 1580. Gerard, who was the first to publish an illustration of the plant,[1] had himself represented on

FIG. 509.—John Gerard, holding a branch of the potato, bearing flowers and fruit. (From Title-Page of Gerard's *Herball*, Ed. 1633.)

the title page of his Herball holding a flowering branch of the plant in his hand (Fig. 509).

[1] In Gerard's Herball, 1st Edition, 1597, p. 781 (p. 927 of the edition of 1633), under the name *Battata Virginiana*. Bauhin, in his Phytopinax (p. 89, 1596), described the potato under the name, *Solanum tuberosum esculentum*, and classed it (correctly) as a Nightshade. Bauhin's illustration is not as correct as Gerard's. Linnaeus, in accordance with his system of binomial names, adopted the first two of Bauhin's names as the botanical name of the potato, and this name has persisted unchanged until the present.

While Gerard was perhaps the first to *publish* an illustration of the potato, there is a colored plate of the plant, accompanied by a description by Clusius,[1] preserved at the Musee Plantin-Moretus. Clusius received two tubers and a seed-ball in 1589 from Philippe de Sivry, Seigneur of Waldheim and Governor of Mons, who in turn had received them from Italy. According to Roze, all the potatoes which were cultivated in Austria, Germany, Switzerland, and France at the end of the sixteenth century, came from those two tubers and the seeds in the seed-boll. The varieties from this stock had reddish tubers and purple flowers, while the potatoes introduced into Great Britain about 1597 by Gerard (and described by Caspar Bauhin in 1596), had yellow tubers and violet or nearly white flowers.

It was the horticulturist Antoine-Augustin Parmentier who introduced the cultivation of the potato into France, during the famine of 1769. From this fact, the first popular French name of the potato was *parmentière*—the name *pomme-de-terre* being introduced later.

In the New World *Solanum tuberosum* has never been found growing wild. Darwin found a wild species (*Solanum maglia*) growing in the sand on the southern coast of Chile. The tubers of the plants found by Darwin were not over two inches in diameter, and were of inferior quality. There seems to be little doubt that the true *Solanum tuberosum* is indigenous in the high Valleys of Chile, and Peru; it is reported to have been introduced into cultivation in that part of the eastern United States which now includes Virginia and North Carolina in the latter half of the sixteenth century. Strange to say, the cultivation of the

[1] Charles de L'Ecluse (Carolus Clusius) was born in Arras, French Netherlands (now Artois, France), in 1526, and died in Leiden in 1609. From 1573–1587 he was director of the Imperial Botanical Garden, at Vienna. From 1593 until his death he was professor at the University of Leyden. He translated Dodoens's great Flemish herbal (*Cruydt-boeck*) into French (1557). His most famous work is the *Rariorum Plantarum Historia* (1601). He was the teacher of Lobelius and of Jean Bauhin. He was one of the first botanists to study plants for their own sake, rather than for their economic or medicinal uses. Meyer, the historian of botany, says of Clusius: "No predecessor or contemporary has enriched the knowledge of plants with more new discoveries, or has set forth and described his discoveries with such ability."

potato did not spread northward from Virginia, but was introduced into the New England provinces by Presbyterian emigrants from Ireland about 1719.[1] It is reported to have been served at a dinner at Harvard College as early as 1707, but only as an unusual delicacy. There are now under cultivation several hundred named varieties, though some of these are inferior and many of them are no doubt synonyms of others.

While the plant is chiefly propagated vegetatively, by planting tubers or portions of tubers, it also, under certain circumstances, sets seed. Whether propagated by tubers or by seeds, *mutations* (*Cf.* pp. 962 and 1011) frequently occur, giving rise to departures from the parent stock, and not infrequently to distinct forms of commercial value. As a result of bud sporting, white-skinned tubers, for example, are sometimes found in a hill of a red-skinned variety. Such a phenomenon is often called "mixing in the hill." New forms may also be produced by hybridizing.

It was by planting potato seeds that Luther Burbank, in 1871, while yet a boy, originated the well known Burbank potato. He secured twenty-three seedlings from one potato "ball," or fruit; each of these seedlings was unlike the others, and all were unlike the parent plant. One had such deep-set "eyes" as to unfit it for culinary use; another decayed very soon after being dug; but one of the seedlings produced tubers that were far superior to the parent and to any of the varieties then on the market. These tubers, propagated vegetatively, became the ancestors of the Burbank potato.

Horticultural varieties have a tendency to "run out" unless the planter selects, as "seed," tubers true to type. Potato diseases may also be a factor in causing varieties to run out. Some varieties doubtless disappear because the market demand for them ceases on account of the introduction of a new and better variety, or for other reasons.

When a potato seed is planted the seedling follows the usual course of development; the root begins to develop first, thus insuring an adequate supply of water, the fundamental need of all plants; the persistent, leafy cotyledons expand somewhat and become green, thereby initiating early the photosynthetic activity of the plant; then the epicotyl elongates and the first foliage

[1] Hazlett, Charles A. History of Rockingham County, New Hampshire, etc., p. 506. 1915.

leaves begin to expand (Fig. 510). In about six or eight weeks the first runners or stolons develop in the axils of each of the cotyledons, and the first tubers are formed by the enlargement of the tips of these stolons (Fig. 511).

When tubers are planted a main underground stem develops from one of the buds in an eye. The length of this stem depends on the depth of planting, and from its nodes it sends out branches

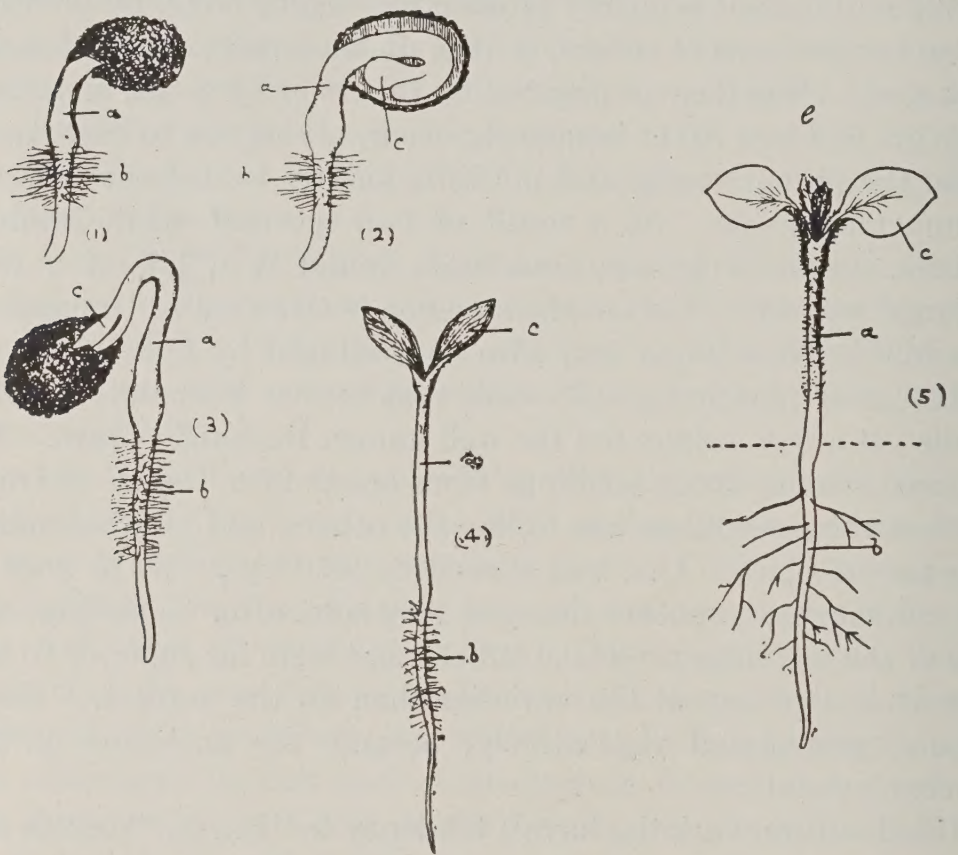


FIG. 510.—1, Potato seed germinating. 2, Section through the same, showing position of the cotyledons and endosperm (shaded). 3, Seedling nearly free from seed-coat. 4, Seedling erect (10 days old); *a*, hypocotyl; *b*, root; *c*, cotyledons. 5, Seedling 16 days old; *e*, plumule. (After Percival.)

or stolons which also form terminal tubers (Fig. 512). The seed-tuber should, therefore, be planted 5–6 inches deep in order that it may have room to form a node for as many vigorous stolons (bearing tubers) as the plant can support or nourish. If the seed-tuber is planted too deep the tubers formed on the stolons from the first two or three nodes are likely to be undersized and otherwise inferior, as the moisture and temperature conditions are not favorable. If planted too shallow (less than 3 inches deep) the

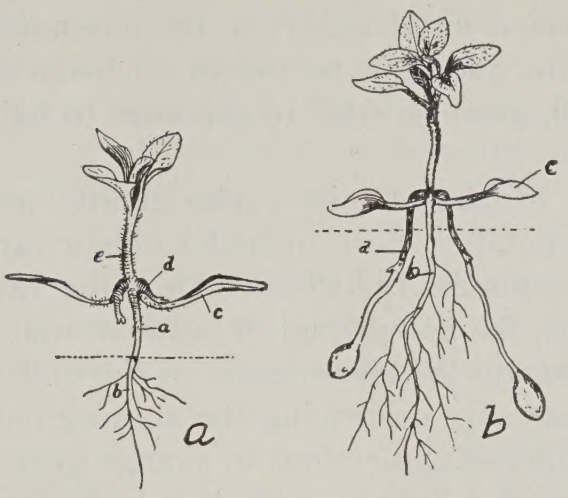


FIG. 511.—Left, potato seedling 26 days old; *d*, the young first stolons, arising as branches in the axils of the cotyledons (*c*). Right, seedling 10 weeks old. The stolons have penetrated the ground, and two small tubers have formed at their tips. (After Percival.)

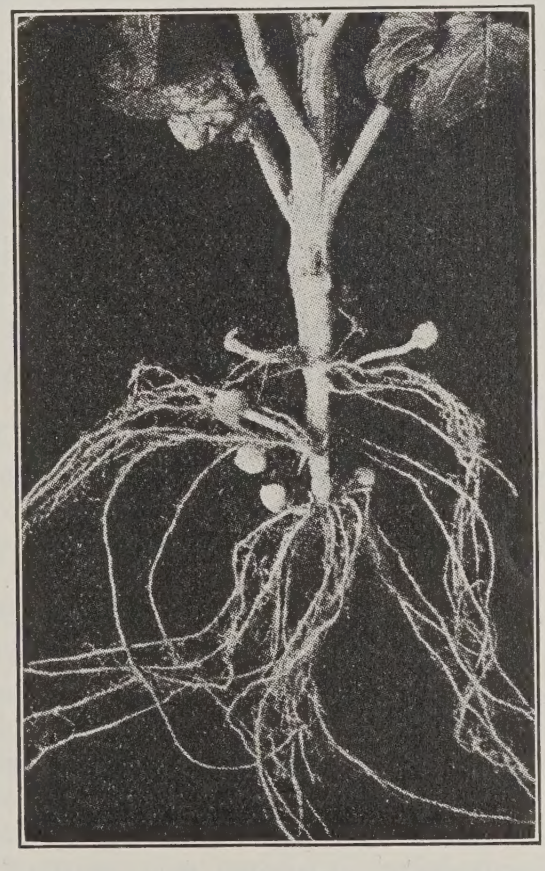


FIG. 512.—Plant of the Irish Cobbler variety of potato grown from a seed-tuber. Young tubers have just started to form at the tips of the stolons. (After Charles F. Clark, U. S. Dept. Agr.)

tubers are affected unfavorably by the fluctuations of moisture and temperature, and there results an excessive number of small, often branched, greenish (due to exposure to light), and scabby tubers.[1]

The length of the stolons varies greatly according to the variety, being notably short, in Irish Cobbler variety, and much longer in, for example, the Charles Downing variety. Thomas Andrew Knight, the noted English horticulturist, was one of the first to demonstrate the stem-nature of the underground, tuber-bearing stolons.[2] By destroying the above-ground branches he induced the underground stolons to change their habit and grow up into the air and light. From this he concluded that they "are very similar in organization to the stem of the plant, and readily emit leaves and become converted into perfect stems, in a few days, if the current of ascending sap be diverted into them."[3]

Structure of a Tuber.—If a tuber is cut lengthwise (or across) four fairly distinct regions may be observed,[4] as follows (Fig. 513):

1. The outer, colored, and (in old tubers) suberized *skin*, more or less easily separated from the next inner tissue.

2. The *cortical layer*, (Fig. 514) ⅛–½ inch thick, denser than the inner tissue, and containing vascular bundles and an abundance of starch; it is distinguished by a layer (line in sectional view) of these bundles from,

[1] Gilmore, John W. Quality in potatoes. Cornell Univ. Agr. Exp. Sta. Bul. 230. June, 1905.

[2] In a letter to Dr. Bevan, Knight once said "I have been and am still engaged in some experiments on the potato, which plant has given me more physiological information than all the remainder of the vegetable world; and where it has not given me the information I wanted, it has directed me where to find it."

[3] It is fortunate for agriculture that some of Knight's conclusions are not wholly correct, else planting would, indeed, be a most laborious process, for in 1822 (Trans. Hort. Soc. London **4**: 447) he states that potatoes, being "shoots, or branches, which have grown thick instead of elongating," gardeners should take pains to plant the tubers right side up with care. Cf. Gager, C. S. Tuber-formation in *Solanum tuberosum* in daylight. Torreya **6**: 181–186. Sept. 1906. Also, p. 293, preceding.

[4] These regions were clearly illustrated and described by Coudon and Boussard. Recherches sur la pomme de terre alimentaire. Ann. Sci. Agron. Ser. 3. **3**:250–291. 1897. East, Univ. Ill. Agr. Exp. Sta. Bull. 127.

3. The *external medullary layer* (Fig. 515), comprising the greater part of the starchy tissue.

4. The *internal medullary layer* (Fig. 515), consisting of a main central portion which appears to send out branches to each eye. The cells of this layer contain mostly water and are relatively poor in starch.

Proceeding from the skin inward, the amount of starch decreases, while the amount of water and nitrogenous matter increases; although the outer tissues are richer in *protein nitrogen.*

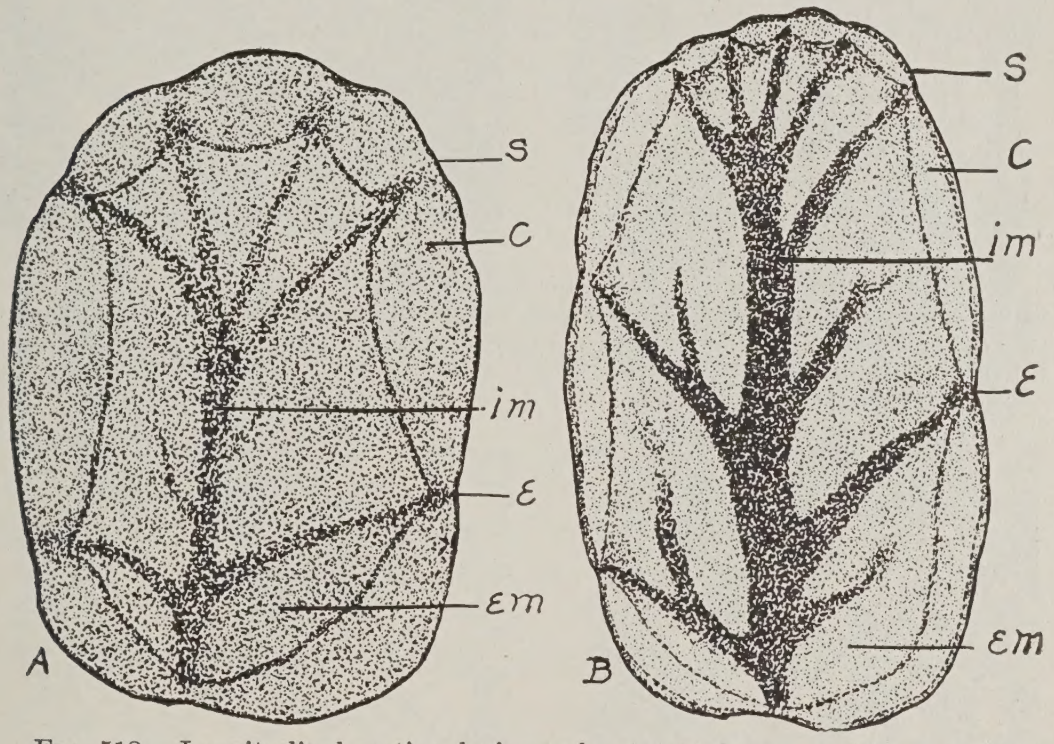


Fig. 513.—Longitudinal sectional views of potato tubers. *s*, skin; *c*, cortical layer; *em*, external and *im*, internal medullary layers; *e*, eye. A, tuber of good quality, with large cortical and external medullary layers, and small or finely divided internal medullary layer. B., tuber of poor quality; with small cortical layer and large, thick internal medullary layer. (After East.)

Hence the culinary advantage of boiling potatoes with the skin on. *Mealiness* of boiled potatoes is caused by the enormous amount of swelling of the starch grains, which ruptures the cell-walls. When the external medullary layer is poor in starch the cells do not burst and the potato is "soggy;" when the internal medullary layer is unusually large in extent (Fig. 513, *B*), the external medullary layer is not uniform in starch content, and the boiled tuber has areas which are hard, causing the lumps in mashed potatoes.

Tubers within Tubers.—In rare cases potato tubers exhibit the phenomenon of ingrowing sprouts, that is, one or more of the buds

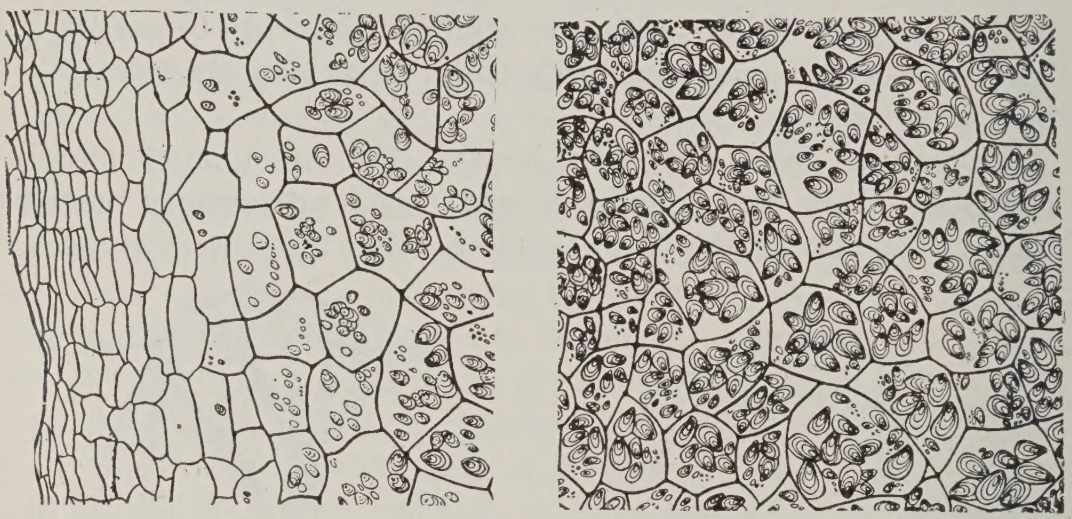


FIG. 514.—*Left*, Section of the outer portion of the cortical layer of a potato tuber, showing the cellular structure and the starch grains in the cells; *Right*, section of the inner portion of the cortical layer. These sections are from the same tuber as those in Fig. 515. (After East.)

FIG. 515.—*Left*, Section of potato tuber near the vascular bundles, showing a portion of the external medullary layer; *Right*, section of the internal medullary layer. These sections are from the same tuber as those in Fig. 514. (After East.)

of the eyes grows in and through the tissue of the tuber. In such cases the sprouts tend to behave as rhizomes in the ground, and tuberize freely, not only at their tips but back from the tip (Fig.

516).[1] Stewart[2] has also described interesting cases showing that the tubers formed on ingrowing sprouts may grow to a considerable size, rupturing the tissues of the parent tuber and protruding.

Aerial Tubers.—Not infrequently, as noted above, tubers are produced from the aerial portions of the stem, especially in diminished light or in darkness (Fig. 517). In regeneration experiments with potato leaves a tuber is, in some cases, devel-

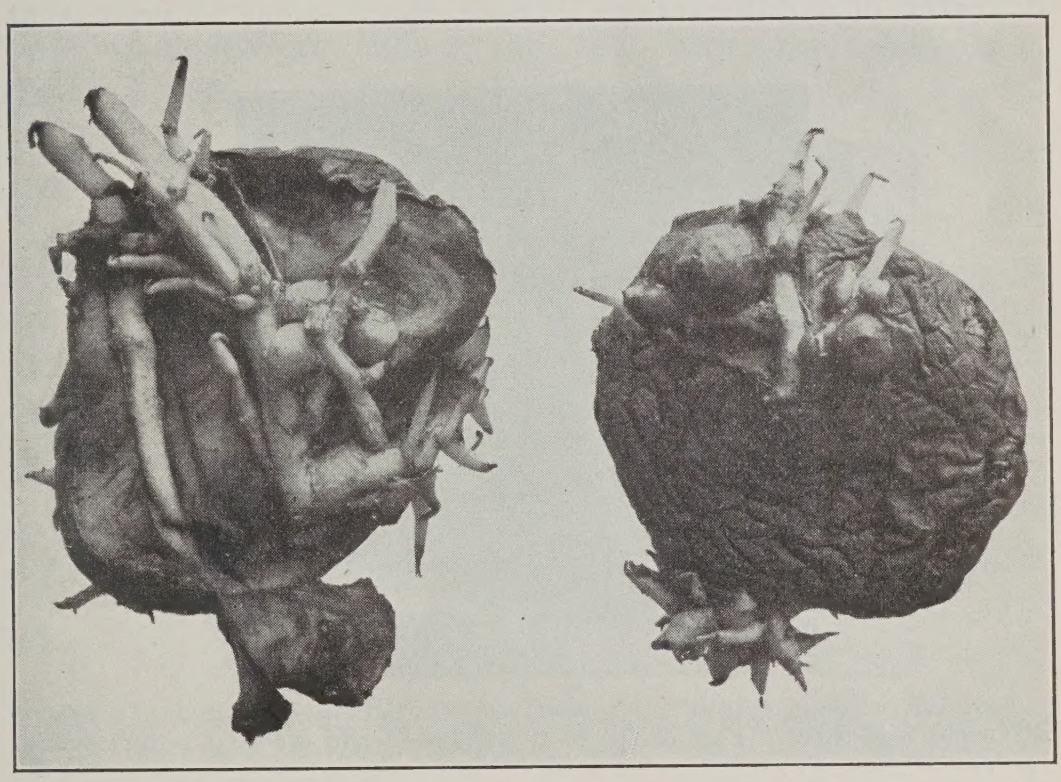


FIG. 516.—Potato tubers with ingrowing sprouts. The figure at the right shows ingrown sprouts and small tubers emerging through the skin of the old tuber. The figure at the left is a dissection showing the tuberization of some of the ingrown sprouts.

oped directly at the end of the leaf-stalk; in other cases roots are formed (Fig. 204).

Correlation with Shape.—Just as tuber-formation is a specific characteristic of *Solanum tuberosum*, so also is the shape of the tuber a varietal characteristic, some varieties (*e.g.*, Irish Cobbler,

[1] Gager, C. Stuart. Ingrowing sprouts of *Solanum tuberosum*. Bot. Gaz. **54**: 515–524. Dec., 1912. Brooklyn Botanic Garden Contributions, No. 5.

[2] Stewart, F. C. Tubers within tubers of *Solanum tuberosum*. Brooklyn Bot. Gard. Memoirs. **1**: 423–426. July, 1918.

Triumph) having globular ("roundish") tubers, others (*e.g.*, Green Mountain, Burbank) having oblong tubers, while still others (*e.g.*, Early Rose, Early Ohio), have tubers of intermediate shape ("roundish oblong," "round-flattened to short oblong," etc.). A Russian investigator, Renski,[1] at the Experiment Field at Poltava, Ukrainia (Russia), recorded observations for many years on the relation between starchiness and longitudinal diameter of potato tubers. These observations showed that

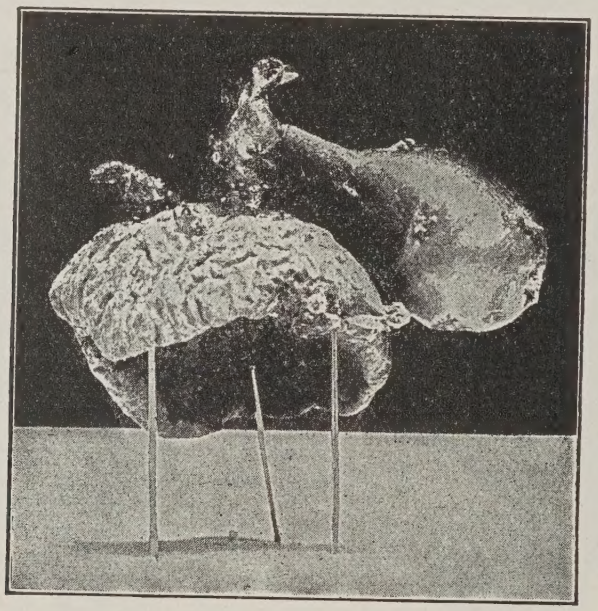


FIG. 517.—Young potato tuber, developed (in light) as a branch of a sprout of an old seed-tuber. Part of the food elaborated and digested in the leaves of the parent plant was translocated down the leaf-stalk and stem, and stored in the older tuber, part of which is shown in the figure. After this piece was cut off, the stored food began to be digested and translocated to the developing "eye" or bud, accompanied by the development of the latter into the young tuber. Ordinarily such changes, in the potato, occur only underground and in the dark.

globular shaped tubers have a much higher starch content than oblong ones. The average starch content of many varieties with oblong tubers was 18.5%, while in globular ones the starch content was 23.5%. One must not hastily conclude that the amount of starch present determines the shape of the tuber; all that we know is that there is a correlation between these two variables.

[1] Renski, M. D. Correlation between longitudinal diameter of potato tubers and their starchiness. Russian Jour. Exp. Landw. **11**: 228. 1910. Abstract in Exp. Sta. Rec. **24**: 439. 1911.

The "Eyes."—Examination of a mature tuber will show that the "eyes" are more numerous at one end than at the other (Fig. 518); this is the morphological *apex* of the tuber, and the withered remains of the rhizome that bore it will often be found attached to the opposite end. The so-called "eyes" are buds in the axils of aborted leaves. There is always a central or apical bud surrounded by several smaller lateral buds. Often tubers are found to have branched, thus producing lateral knobs, which are very undesirable from the culinary, and therefore from the commercial point of view.

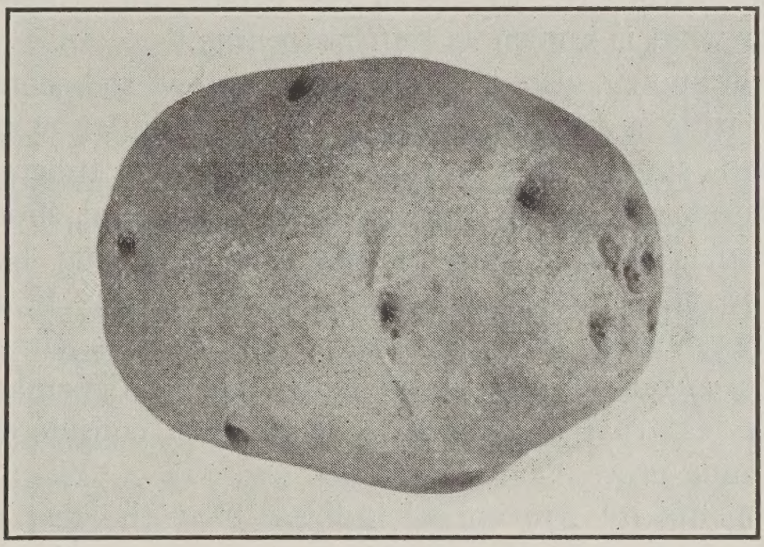


FIG. 518.—Mature tuber of *Solanum tuberosum*. Note the greater frequency of the "eyes" near the apical (right hand) end. (Photo by Folsom. Courtesy of Maine Agr. Exp. Station.)

Cause of the "Rest-period."—All parts of plants have, as a rule, what is commonly known as the "rest-period (*Cf.* pp. 702, 788)." We are familiar with this in seeds and in deciduous trees. Even in the tropics many plants have alternate periods of growth and rest. Some investigators have inferred from their observations and experiments that the rest period is a response to changes in the environment, while others have concluded that it is an expression of the hereditary nature of the plant, and largely independent of the environment. The question, in its larger aspects, cannot be discussed here, but a few facts should be noted concerning the rest-period of the potato tuber, since it is of practical as well as of theoretical importance. This is specially the case in

the southern United States where tubers harvested late in the fall are used as "seed" for early crops the following spring.

It is common knowledge that the tubers of most varieties of potato will not grow if planted immediately after they are dug. The period that must intervene (usually several weeks) is called the *rest-period.* It is fairly constant for any given variety. The end of the rest-period is indicated when any considerable number of the stored tubers begin to sprout. When sprouting begins, the tubers are physiologically ready to plant, and further rest is not necessary. During the rest-period certain physiological changes take place within the tissues of the tubers, and these changes constitute what is known as "*after-ripening.*"

It is well known, also, that old potatoes tend to become sweetish, indicating a transformation (by intracellular enzymes) of the stored starch into sugar. Exposure of tubers to low temperatures accelerates this transformation and shortens the rest period. Thus, Müller-Thurgau reported that by storing tubers for one month at a temperature of 32° F. he could materially shorten the rest period. Since this change from starch to sugar is largely, if not entirely, dependent upon change in external temperature, it is not considered as an after-ripening process.

Experiments by Appleman[1] indicate that the rest period is largely determined by the supply of oxygen required for respiration. The oxygen supply to the parenchyma tissue of the tuber is greatly reduced by transformations in the "skin." Immature potatoes have a thin, slightly suberized skin, which is quite permeable to both water and gases. As the tubers mature the layer of suberized cells increases in thickness, and the skin adheres more closely to the underlying tissue. Everyone is familiar with this last fact from the greater ease with which the skin may be removed from new than from old potatoes when preparing them for the table. These changes occur more rapidly under dry than under moist conditions of storage, and it is the suberized layer, only slightly permeable, that shuts off the internal tissues from the oxygen of the air, and thus greatly reduces respiration.

[1] Appleman, Charles O. Study of rest period in potato tubers. Maryland Agr. Exp. Sta. Bul. No. 183. 1914. Appleman's phraseology is here freely followed.

Reasoning on these facts, it occurred to Appleman that sprouting, or the growth of the buds, was checked by this exclusion of oxygen. To test his hypothesis he made the following experiments. Choosing McCormick potatoes harvested on November 4, he planted them at once in the greenhouse in soil, sawdust, and sphagnum, but in no case did any of the buds begin to sprout until January 18, and general sprouting did not begin until February. This experiment was repeated on three successive years, and it was thus determined that the normal rest-period for the McCormick variety of potatoes is (for Maryland) about 90 days. It was also found that the degree of previous suberization or "corking," of the skin greatly influenced the length of time before tubers with the skin intact begin to sprout.

To test the effect of removing the skin on the length of the rest period, Appleman removed the skin from a number of normal tubers at various stages of the rest-period, and then planted the stem ends (the end where the tuber was attached to the stolon) in wet soil or sawdust, covering the opposite or apical ends ("seed-ends") with two or three inches of excelsior, kept constantly wet. This method allowed the freest access of oxygen to the seed-ends. By this experiment it was found that removal of the skin at *any* stage of the rest-period will cause the tubers to sprout within ten days, if other conditions are favorable (Fig. 519). Appleman also determined that the elimination of the rest-period by removing the skin was not due to the greater ease with which water could be absorbed, for pared tubers in dry storage would sprout much earlier than those with the skins on. In one experiment mature tubers harvested November 4 had their skins removed on November 7. After lying in a moist chamber four days they were placed in paper sacks and stored in a cupboard in the laboratory. At the end of 64 days, of those with the skins on only 30% had sprouted, while of those with the skins removed all had sprouted.

By further experiments Appleman determined that the vigor with which the tubers respire, as measured by the amount of carbon dioxide given off, decreases as the tubers increase in age—that is, as the suberized tissue increases in thickness and the skin adheres more closely to the underlying tissue. From these experiments the conclusion is that the rest-period in potato tubers

is not firmly fixed and hereditary, since it can be entirely eliminated by any means which facilitates the continued supply of oxygen to the tissues under the skin.

As a practical application of the knowledge obtained by these experiments, Appleman[1] has suggested that the territory for

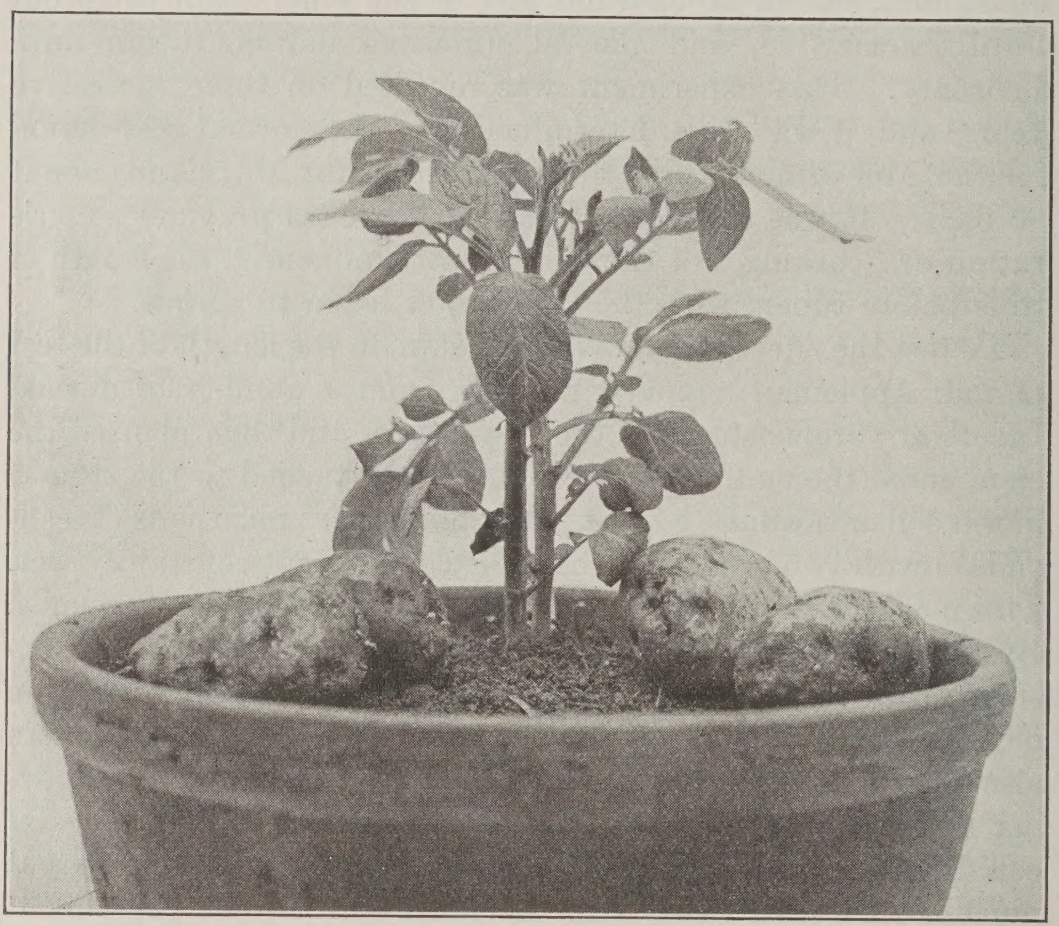


FIG. 519.—Potato plant photographed on November 24. This plant was produced by a tuber harvested on October 15 and induced to sprout at once by removing the skin. The tubers on the left of the plant were sprouted at the same time, but planted in soil before any roots were produced. The tubers on the right were planted in the soil without removing the skins. The two latter sets of tubers failed to produce plants. (After Appleman. Maryland State Agr. Exp. Sta.)

growing a second late crop for early spring seed might be profitably extended by resorting to only slightly artificial means to shorten the rest period. The part of the early crop intended for seed should be dug late in the day, and preferably when the

[1] Appleman, C. O. Physiological basis for the preparation of potatoes for seed. Maryland Agr. Exp. Sta. Bul. No. 212. 1918.

ground is moist from a recent rain. The tubers should then be *at once* transferred to a warm shady place, spread out on the ground in thin layers, and covered with moist gunny sacks or moist excelsior. Keeping the tubers from drying retards the formation of the corky layer of the skin, and the loose covering allows ready access of oxygen.

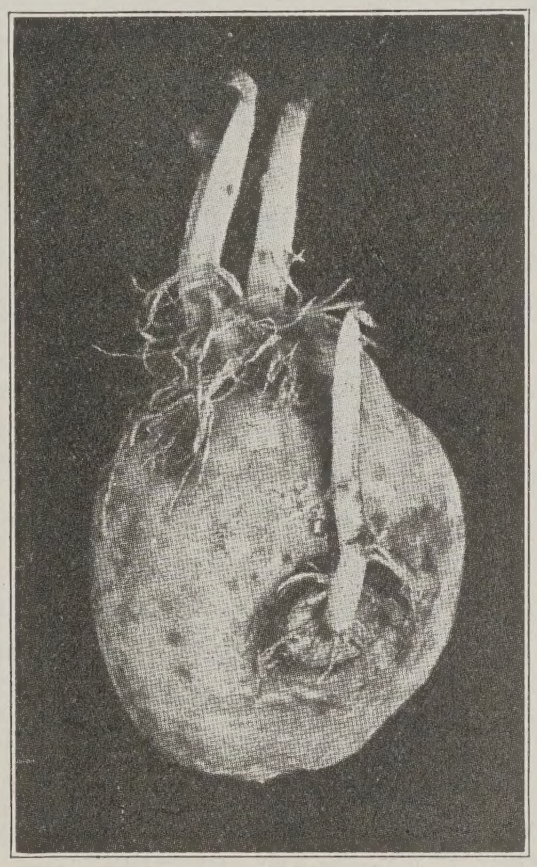


FIG. 520.—Experiment to show the counteracting of the inhibiting effect of apical buds of potato tubers by more favorable external conditions. A deep furrow was cut around the basal eye close enough to allow easy access of oxygen and moisture to the tissue near the bud. The vital connection with the terminal eyes was not severed, for similar furrows some distance from the basal eyes will not remove the inhibitory influence of the terminal eyes. (After Appleman. Maryland Agr. Exp. Sta.)

Influence of Terminal Buds on the Sprouting of the Other Buds.—When a potato "sprouts," that is, when the "eyes" begin to grow, either in storage or after planting, those on the apical (distal) end begin to grow first, and if they continue normal vigorous growth, those on the basal end will not grow at all. It would seem as though the growing buds on the apical end *inhibited* the growth of those farther back on the tuber, and a

careful experimental study of the problem indicates that such is the case. Just how this inhibition is brought about—the mechanism of it—is not known, but it would appear as though some inhibiting substance was secreted by the growing buds at the tip and translocated to the buds farther back on the tuber, thus inhibiting their growth.

The inhibiting effects of the apical buds may be entirely overcome if the basal buds can be more favorably related to external influences than they are normally. Appleman found that buds in contact with a moist surface will often sprout first regardless of their location on the tuber. If a channel is cut around a middle or basal eye close enough to allow easy access of oxygen and water to the tissue surrounding the girdled buds, the latter will grow out as quickly or more quickly than the (ungirdled) apical buds on the same tuber. (Fig. 520.)

It is of interest to note that the growth of the central bud of an eye, in a similar manner, inhibits the growth of the lateral buds of the same eye. If we destroy the central buds the lateral ones will grow; if we destroy all the buds of the apical eyes the eyes further back will sprout.

Preparation of Tubers for Seed.—It hardly needs stating here that, in raising potatoes by planting tubers or pieces of tubers, every piece, in order to produce a plant, must have an eye. It is also well known that it is not necessary to plant entire tubers. The question therefore arises, is there a best way to cut the seed tubers and, if so, what is the best way? It was ascertained by experiment that if tubers are cut lengthwise (from apical to stem end) and placed under conditions favoring sprouting, only the buds of the apical eyes will grow. This, of course, might have been inferred from what has been said above. The actual experiment confirms the inference.

If, however, the tuber is cut into a number of slices, approximately at right angles to the long axis, at least one bud will sprout on each slice that contains an eye (Fig. 521). It would appear that the inhibition of the lower buds has been removed and the growth process released for all the buds.

From these experiments it is evident that *it would be wasteful to cut potatoes lengthwise for planting.*

Effect of Size of Seed Piece on the Crop.—This is one of the most important considerations in preparing tubers for planting. Many experiments have been made in different countries to ascertain whether the size of the seed-piece affected the size of the crop, and the results of these experiments show that, without

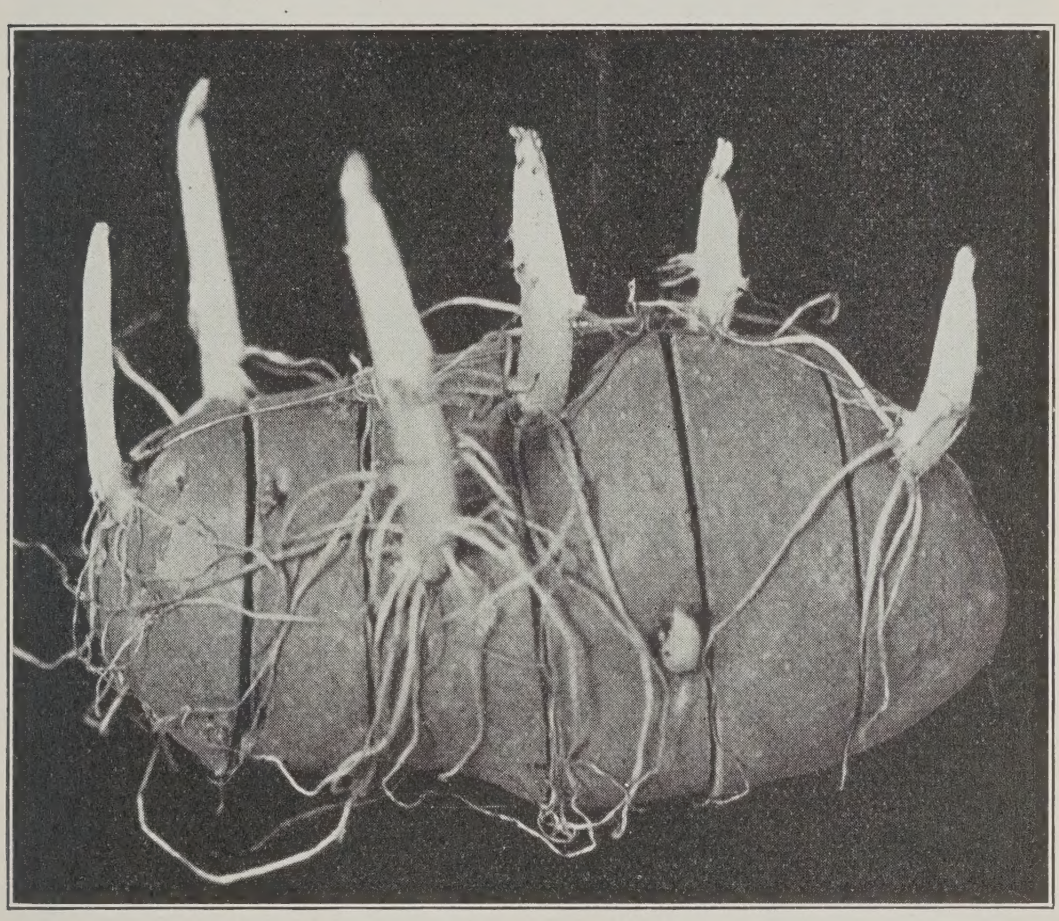


FIG. 521.—Experiment to show the release of the growth processes in ends of a potato tuber when the other buds are isolated from the terminal buds. After the normal rest period was over the tuber was cut into slices one-half inch thick, and allowed to sprout in wet sawdust. Each slice produced at least one sprout. When similar tubers were cut lengthwise into quarters so that the lower buds were still under the influence of the apical buds, sprouts appeared only in the apical eyes. (After Appleman. Maryland Agr. Exp. Sta.)

question, the larger the seed piece the more vigorous is the sprout and the better the yield. This is graphically shown in figure 522. It has also been demonstrated that, when whole potatoes are planted as seed, the larger the tuber the larger the number of sprouts that will develop, and the larger the yield (Fig. 523).

As Appleman[1] has pointed out, the fact that the yield increases directly with the weight of the seed piece does not mean that it would always be profitable to increase the amount of seed up to the maximum, for other considerations enter in. Thus, by increasing the number of hills per acre, the size of the seed pieces

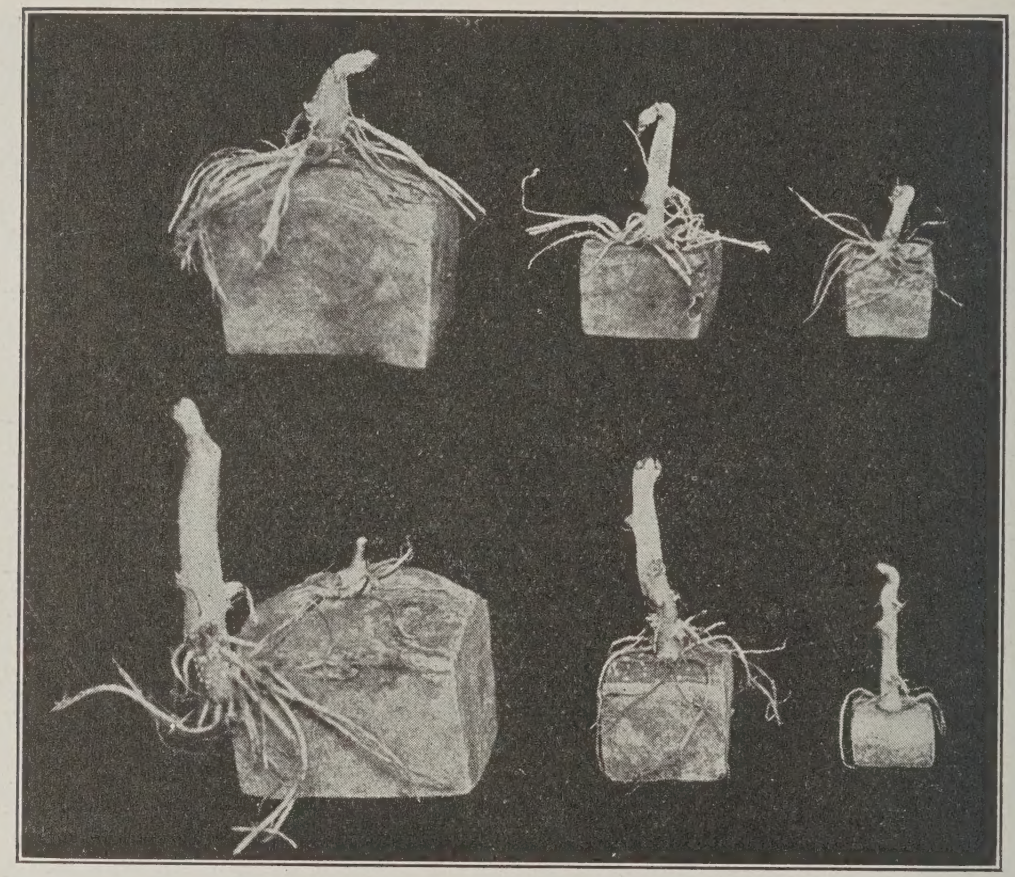


FIG. 522.—Experiment to show the effect of the size (weight) of the seed-piece of a potato tuber on sprouting. Below a certain minimum weight of seed-piece the vigor of the sprouts decreases as the piece is reduced in size. In this experiment thirty tubers of the McCormick variety of about the same size were selected, and the middle eye from each tuber was cut out. Ten of the eyes were on 1½ inch cubes, ten on ¾ inch cubes, and ten on ½ inch cubes. The blocks chosen for this illustration represent (below) the maximum and (above) minimum growth in each lot.

may be decreased without loss to the crop taken as a whole, though the yield per hill or per plant would be less. Moreover, the increase of yield with increase in size of seed piece is not uniform throughout the entire range of sizes; after the larger sizes are reached the increase in yield per unit increase in weight

[1] Maryland Agr. Exp. Sta. Bul. 212. 1918. Pp. 92–95.

of seed pieces is less than with the smaller pieces. The relative cost of the seed tubers is also a factor.

During the World War the use of parings (peeled skin) with eyes attached was recommended, so that practically all of the

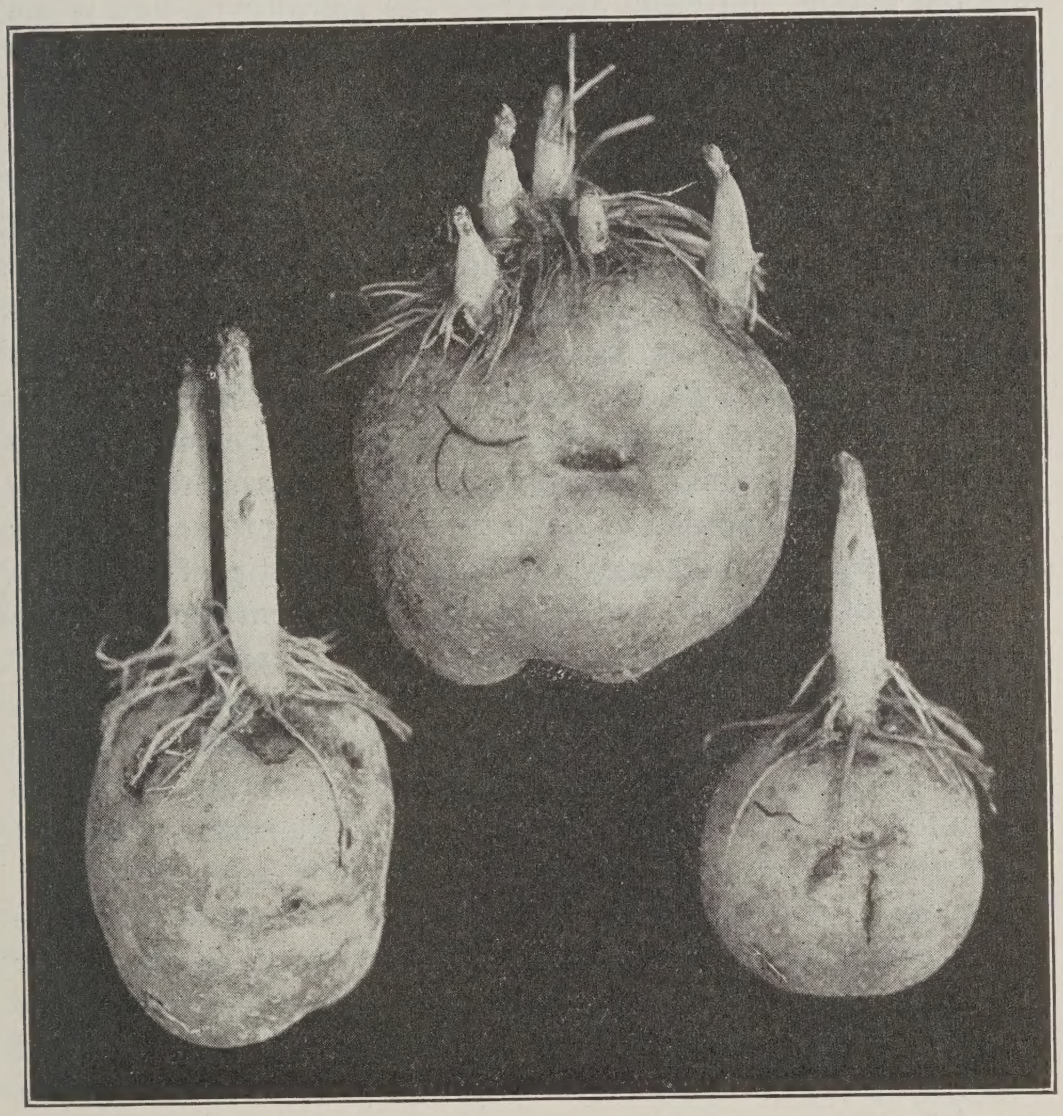


FIG. 523.—Relation between the size of a seed-tuber of potato and the number of buds that will grow out when the tubers are sprouted under good growing conditions. These are Irish Cobbler potatoes sprouted in wet saw-dust. (After Appleman, Maryland Agr. Exp. Sta.)

flesh of the tuber could be used for food. Appleman showed experimentally that the yield from using parings as seed was too small to pay for the use of the ground and the labor involved. Thus, with McCormick variety of potatoes, when the average weight of the seed piece was 1.75 ounces (24.96 bu. per acre), the

actual yield per acre was 346 bushels; but when the average weight of the seed piece (parings) was only 0.08 ounces (1.10 bu. per acre), the actual yield per acre was only 18 bushels.

When cutting the seed tubers they should be cut so as to separate the middle and basal eyes from the apical eyes, and if the central sprout of an eye is destroyed or if an eye is bisected more spouts will result from it, since the inhibiting action of the central bud will be removed from part of the lateral buds. It follows, from what has been said above, that buds near a cut surface will grow more quickly than those farther removed, and that it is not essential that each seed piece should have an apical bud.

The Potato Leaf.—The pinnately lobed or dissected leaves, without stipules, are alternate on the stem. Lutman[1] has called particular attention to the marginal leaf-vein, formed by the fusion (*anastomosing*) of the lateral veins that branch off from the midrib. This marginal vein, nearly continuous around the entire leaf-margin, is composed of sieve tubes and from one to five or six tracheids. It is strongly developed at the tip of the blade where it unites with the end of the midrib to form what Lutman describes as a tangled mass of vessels. At the base of the leaflet the marginal vein does not fuse with the midrib, but continues parallel to it along the leaf-stalk, and supplies the decurrent portion of the blade. Thus the marginal veins of all the leaflets are united to form a continuous vein around the entire margin of the blade.

The water pores, referred to in Chapter IV, are confined to the region at or near the leaf-margin, and open on the upper surface or at the very edge. They are all connected with the marginal vein. The water pores are similar in structure and origin to the ordinary stomata, but larger. It is commonly stated that the guard-cells of water pores do not open and close as do those of ordinary stomata, but Lutman finds that this is not the case with the water-pores of the potato leaf (*Cf.*, p. 59).

Stomata occur on both surfaces of the leaf, the number per square millimeter varying with the size or age of the leaf, and being greater on the under than on the upper surface. Lutman's count for a medium sized tip-leaflet was 400 per sq. mm.

[1] Lutman, B. F. Vermont Agr. Exp. Sta. Sci. Contrib. 1. Burlington, Vt. Oct., 1922.

for the under surface, and an average of 110 per sq. mm. for the upper surface, or total numbers of 348,000 and 95,700 stomata respectively.

Potato Diseases.—Forty or fifty years ago the chief enemy of the potato was the "potato bug" (Colorado potato beetle), which, prior to our Civil War (1861–65), seemed content to feed on another species of *Solanum* (which grew wild as far north as southern Colorado), and on other Solanaceous plants. Gradually this beetle spread eastward, feeding chiefly on the cultivated potato and becoming one of the chief enemies of the crop. More recently a number of destructive diseases have made the potato a very precarious crop, especially in certain sections. Among the more serious diseases are the following. The name of the fungus causing the disease is given in a parenthesis following the name of the disease.

Late blight, downy mildew (*Phytophthora infestans*).

Scab (*Oöspora scabies*).

Little potato, rosette, stem rot (*Corticium vagum* Berkley & Curtis *var. solani* Burt.) (Fig. 372).

Early blight (*Alternaria solani*).

Wilt (*Fusarium oxysporum* and *Bacillus Solanacearum*).

Blackleg (*Bacillus phytophthorus*).

Tip-burn (caused by leaf-hoppers, or by unfavorable environmental condition).

Flowering and Fruiting of the Potato.—While many of the most valuable horticultural varieties of the potato have arisen as seedling sports, it is a well known fact that there is often a complete failure of flowers in a potato field, and often a failure to set fruit with seed, even when the plants come into flower. Often when flower buds are formed they fall off early so that no fruit or potato "balls" develop. Recent studies by Stout[1] show that the non-blooming habit, with the early falling off of the flower buds and flowers when grown under certain conditions, is a direct result of the influence of environment. Thus, varieties which bloom freely in Maine never bloom in New York. Stout says that the production of tubers does not directly prohibit the formation of fruit.

[1] Stout, A. B. Sterilities of wild and cultivated potatoes with reference to breeding from seed. U. S. Dept. Agr. Dept. Bull. No. 1195. March, 1924. See also, Young, W. J. The formation and degeneration of germ cells in the potato. Am. Jour. Bot. **10**: 325–334. June, 1923.

Few varieties of the cultivated potato produce viable pollen, at least in sufficient amount to enable them to function as pollen parents. In many varieties the pollen may start to form but later it disintegrates. According to Young, this disintegration appears to be the result of hereditary pollen sterility; it does not, however, interfere with the normal anthesis of the blossoms. Varieties which do not produce viable pollen may set fruit and

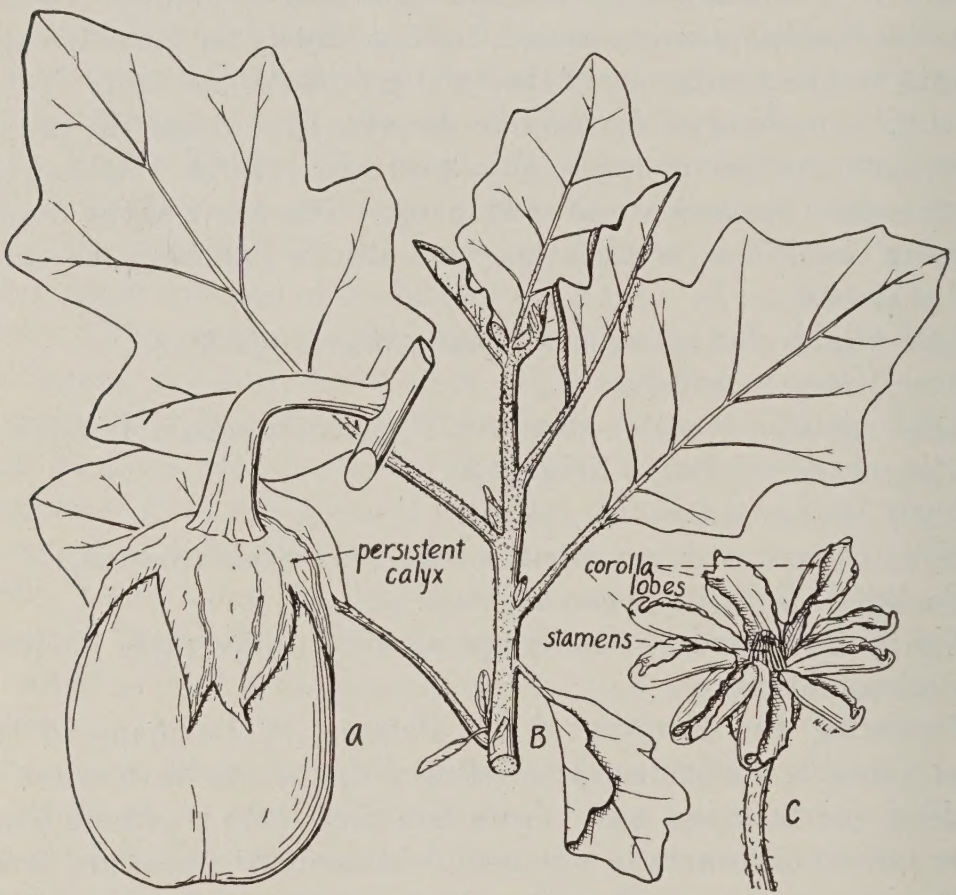


FIG. 524.—Egg-plant (*Solanum melongena*). *A*, mature fruit; *B*, leaves; *C*, single flower. (After Robbins.)

produce seed if the flowers are promptly pollinated with pollen from a variety that produces viable pollen, and provided the environmental conditions do not cause the embryo-sacs to degenerate.

Stout reports that about 14 varieties (including the Rose, Burbank, and Rural groups) may produce fruits without pollination (*parthenocarpic* fruits), but that these fruits seldom, if ever, contain seeds.

EGG-PLANT

Another species of *Solanum* widely cultivated for its fruit is the Egg-Plant (*Solanum melongena*) (Fig. 524). The flowers, in small clusters or single, have a spiny or woolly calyx, and a hairy, purplish corolla. The formation of fruit is often insured by artificial pollination. Since the plant is a native of India it requires a high temperature in order to succeed. The fruit is botanically a berry.

FIG. 525.—Nightshade or Bittersweet (*Solanum Dulcamara*).

Other Solanaceous species, wild in the eastern United States, include the Deadly Nightshade or Bittersweet (*Solanum Dulcamara*) (Fig. 525), introduced from Europe; the common Nightshade (*Solanum nigrum*), and many others, widely scattered throughout the warmer regions of the globe.

TOBACCO

The leaves of *Nicotiana Tabacum* form one of the tobaccos of commerce. The genus is named from Jean Nicot, French ambassador to Portugal, who is said to have sent some species of the genus to Catherine de Medici about 1560. The flowers, arranged in a terminal panicle on a cylindrical stem, average about two

inches in length, and vary in color from white through pink to dark red. The bell-shaped, tubular, or ovoid calyx is 5-cleft, as is also the corolla, whose tube, much longer than the calyx, is swollen below the spreading lobes. The five stamens are inserted on the corolla tube, the ovary is two celled, and the seeds are small and numerous (Fig. 526). Most of the 50 or more species are natives of America, some ten or twelve being found in the United States.

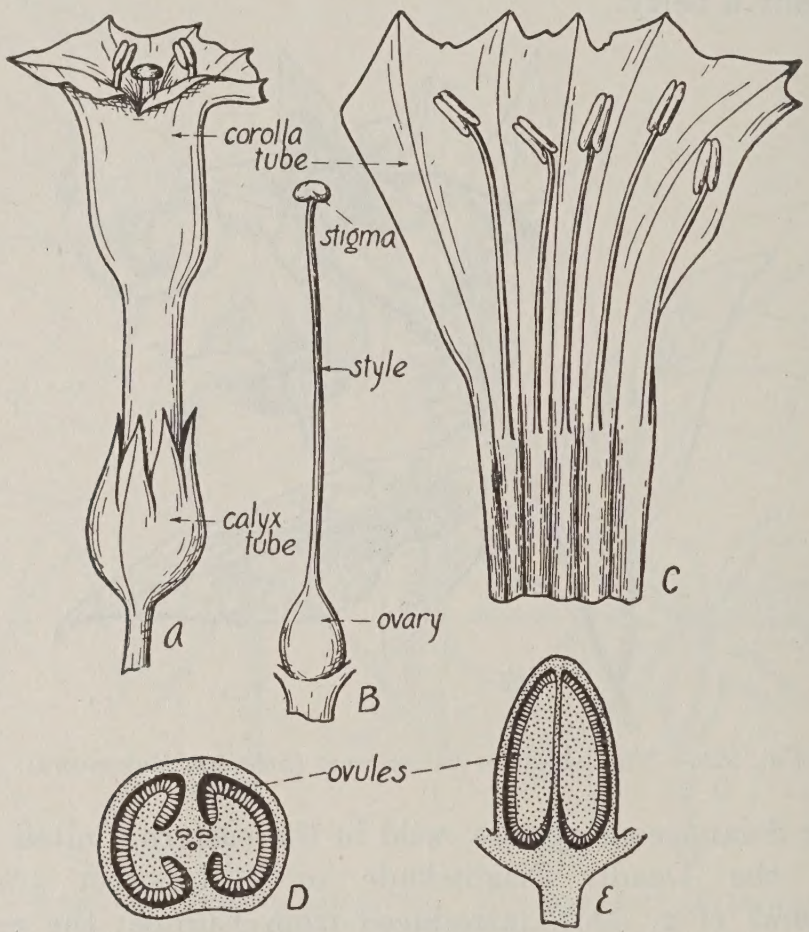


FIG. 526.—Tobacco (*Nicotiana tabacum*). A, flower; B, pistil; C, corolla cut open and spread out flat; D, cross-section of young fruit; E, lengthwise section of young fruit. (From Robbins after Strasburger.)

Wild tobacco (*Nicotiana rustica*), with yellow flowers, found in fields and waste places from Ontario to Minnesota and from New York to Florida, probably originated as an escape from plants cultivated by the Indians. It is native in the New World and is grown commercially in Turkey and adjacent regions.

The discovery of wonderfully wrought tobacco pipes in the tombs of the ancient Aztecs of Mexico shows that the smoking of

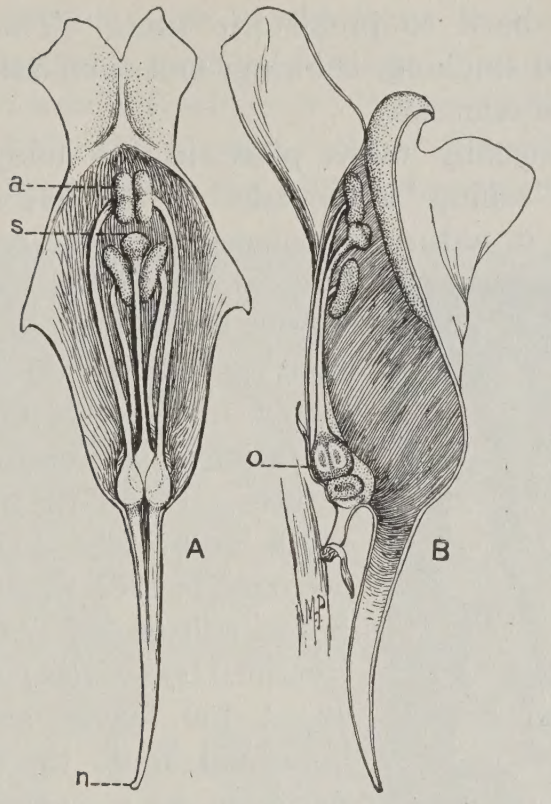


FIG. 527.—Sections of flowers of the toadflax (*Linaria vulgaris*). A, front view; *a*, anthers; *s*, stigma; *n*, nectar-gland. B, side view; *o*, ovary.

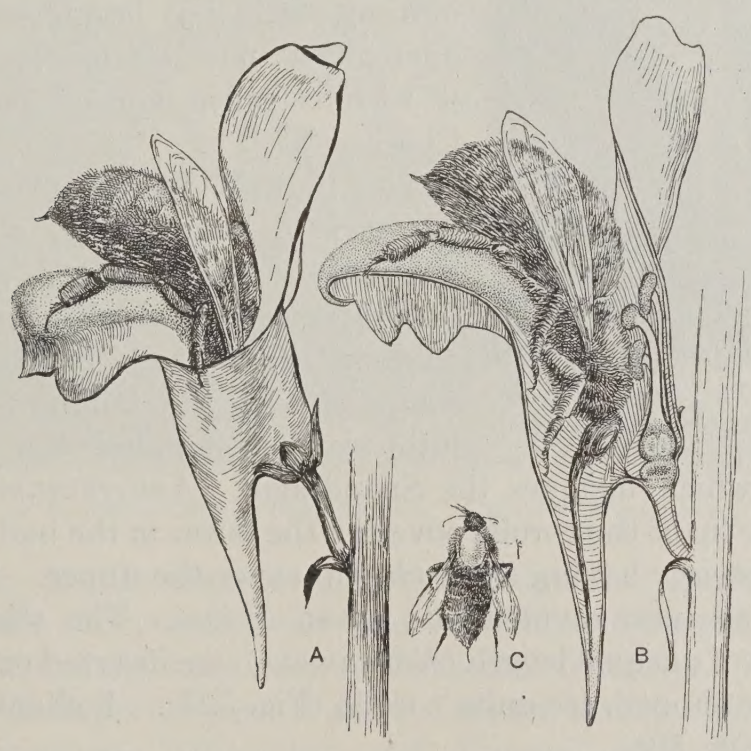


FIG. 528.—Toadflax (*Linaria vulgaris*). *A*, flowers being visited by an insect for nectar. *B*, longitudinal section, showing the insect's proboscis extended down the spur toward the nectar-gland; *C*, insect with a mass of pollen (*p*), rubbed off from anthers onto the dorsal hairs of the thorax during successive visits.

tobacco dates back to prehistoric times. The early Spanish explorers found smoking, chewing, and snuff-taking common in various parts of America.

Pollination usually takes place in the bud, so that close pollination or "selfing" is the rule. If this had always been the invariable rule in nature for tobacco then the result would be a pure ancestral line, and the species should breed true to type from seed (just as plants do from cuttings), except for possible mutations. Such mutations have occurred in rare instances. One of the first recorded and most accurately known mutations occurred in 1907 when there appeared in a culture of seedlings a flat-stemmed (*fasciated*) mutant, bearing about 150 leaves and flowers very abnormal as to the number of their parts, in some cases a single flower having as many as 22 petals. This mutant strain has been used to produce other new strains by crossing it with so-called normal plants (*Cf.* Chapter XL).

FIG. 529.—The toadflax, or butter-and-eggs (*Linaria vulgaris*).

The Figwort Family (*Scrophulariaceae*) is a large group, comprising about 165 genera and as many as 2500 species of wide distribution, including herbs, shrubs, and trees. By some authors the family is divided into two sub-families, the *Antirrhinoideae*, which includes the Snapdragon (*Antirrhinum*) having the upper lip of the corolla covering the lower in the bud; and the *Rhinanthoideae* having the *under* lip cover the upper. The sub-families are also divided into seven *Tribes*. The stamens, of two pairs of unequal length (*didynamous*), are inserted on the tube of the two-lipped, irregular corolla (Fig. 527). Pollination is by insects (Fig. 528).

This family includes one of the most troublesome pasture weeds—the Great, or Common, Mullein (*Verbascum Thapsus*), the common and weedy Toadflax or "Butter-and-Eggs" (*Linaria vulgaris*) (Fig. 529), the Figworts proper (*Scrophularia* sp.) the Beard-tongue (*Pentstemon*), the wild and cultivated Turtleheads

FIG. 530.—*Catalpa bignonioides.* Inflorescence and leaf.

(*Chelone*), the *Paulownia* tree, the Foxgloves (*Digitalis*), the Speedwells (*Veronica*), wild and cultivated *Gerardias* (named from John Gerard, the author of the famous herbal), and others.

The Trumpetcreeper Family (*Bignoniaceae*) includes the Trumpetcreepers (*Bignonia* and *Tecoma*), and the *Catalpa* tree (Fig. 530).

CHAPTER XXXV

SYMPETALOUS DICOTYLEDONS (CONCLUDED)

ORDER, Rubiales

In the Rubiales the leaves are opposite or whorled; it and the following orders all have an inferior ovary.

MADDER FAMILY

The Madder Family (*Rubiaceae*), from which the order is named, comprises nearly 400 genera, and over 5000 widely distributed species. The leaves are almost always entire, and always have stipules. The family contains, in the eastern United States, the Button-bush (*Cephalanthus*), ranging from New Brunswick to Cuba; the Partridge-berry (*Mitchella repens*) (Fig. 531), the Bed-straws (*Galium*), of 20–25 species, and other genera. The genus *Mitchella* is another of numerous plants that illustrate the peculiarity of geographical distribution, previously referred to, namely, the fact that the flora of the eastern United States is more closely related to that of Japan and eastern Asia than is the nearer flora of the western United States. There are, for example, only two species of *Mitchella*—one found in the eastern United States, the other in Japan.[1] Among Rubiaceae of economic importance are the following:

Coffee (*Coffea arabica*, Fig. 532), of which there are several species and varieties, is an evergreen tree, indigenous in the mountainous regions of tropical East Africa, but now cultivated in most warm countries. The striking foliar differences in Congo, Liberian, and Arabian coffee are shown in figure 533. The white flowers (Fig. 534) grow in the axils of the leaves, and the ripe fruit is a red drupe, resembling a cherry and containing two seeds —the coffee "beans" of commerce.

The use of coffee is very ancient. Historical records indicate that it has probably been used in Abyssinia from prehistoric

[1] See page 572 and foot-note, p. 573.

times. It seems likely, however, that in earlier times men depended upon berries gathered from wild plants, and that it came to be cultivated only at a later date; as to just when or where the accounts are conflicting. The botanic gardens at Kew and at Amsterdam have been instrumental in raising seedlings and shipping them to colonies of the respective mother countries. The tree will thrive in soil too poor for other agricul-

FIG. 531.—Partridge Berry (*Mitchella repens*). *Cf.* Fig. 534.

tural crops. De Candolle states that it corresponds, in tropical agriculture, to the vine in Europe, and tea in China.

Cinchona (various species) yields the so-called "Peruvian bark," from which the indispensable drug *quinine* is derived. The plant (Fig. 535) is indigenous on the eastern slopes of the Andes (Bolivia, Peru, and Ecuador), at altitudes of 3000 to 9000 feet in the valleys, and the species that yield quinine are among the

FIG. 532.—Coffee tree (*Coffea arabica*), in fruit. (From Philippine Bur. Sci.)

most recent species of wild plants to be brought under cultivation for economic use. Cinchona Bark was introduced into Europe about 1639 by the Countess of Cinchon, wife of a Spanish Viceroy of Peru, who, by its use, was cured of an attack of malaria contracted in that country. Its use rapidly spread over Europe,

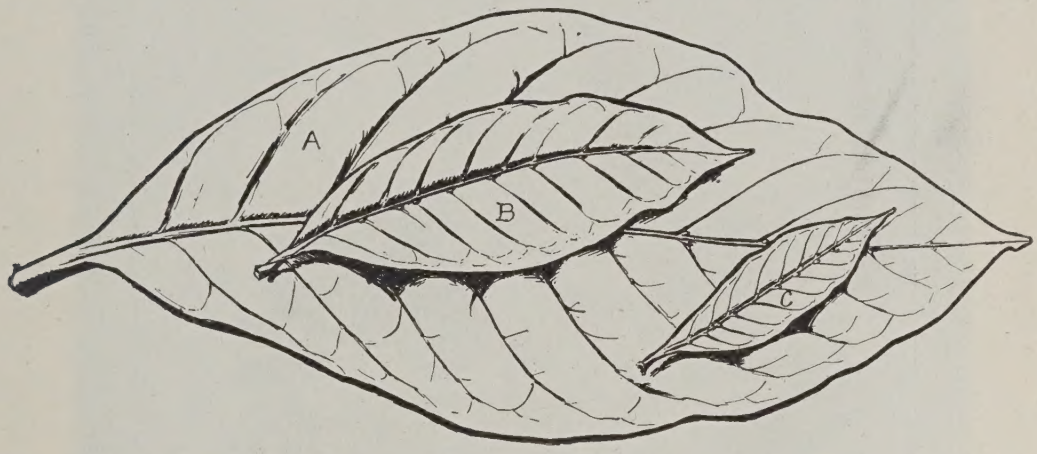


FIG. 533.—Leaves of coffee; *A*, Liberian (*C. liberica*); *B*, Arabian (*C. arabica*); *C*, Congo (*C. robusta*).

but the plant was not known botanically until 1739, when the French astronomer, La Condamine, sent a specimen of it to Linnaeus who, in 1753, named it *Cinchona officinalis*. It was not until another century (1840) that the first living plant was

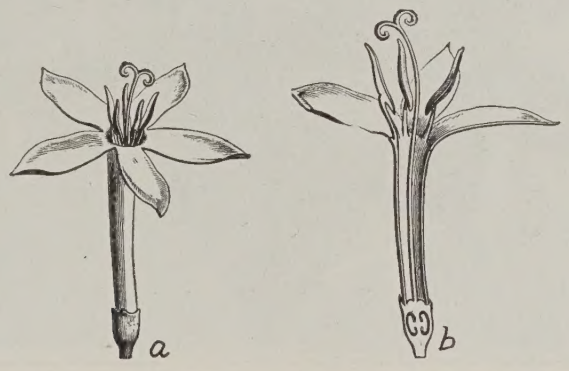


FIG. 534.—Flowers of *Coffea arabica*, entire and in longitudinal section. (After Baillon.) *Cf.* the flowers of *Mitchella repens*, Fig. 531.

grown in Europe, in the Jardin des Plantes, Paris. Shortly thereafter the plant was propagated in large quantities by the Royal Botanic Gardens, Kew, England, and about 1860 its cultivation was successfully introduced by Kew into India, where it soon became one of the most important economic prod-

ucts, being placed on sale at every Post Office, at one farthing a dose.

There are about 30–40 species besides numerous cultivated varieties, hybrids, and races. The cultivation of the original

FIG. 535.—*Cinchona.* Branches of five different species; three in flower, two in fruit. (After Baillon.)

C. officinalis L. has now been largely abandoned in favor of species and varieties of larger yield. One of these is the "yellow cinchona" (Calisaya Bark), *Cinchona Calisaya* Weddell. The full grown trees of this species have a trunk as large as a man's

body, and the chief alkaloid it yields is quinine.[1] Of its many varieties the most important is *Ledgeriana*, obtained in South America by an explorer named Ledger, and now chiefly cultivated in Bengal and Java.

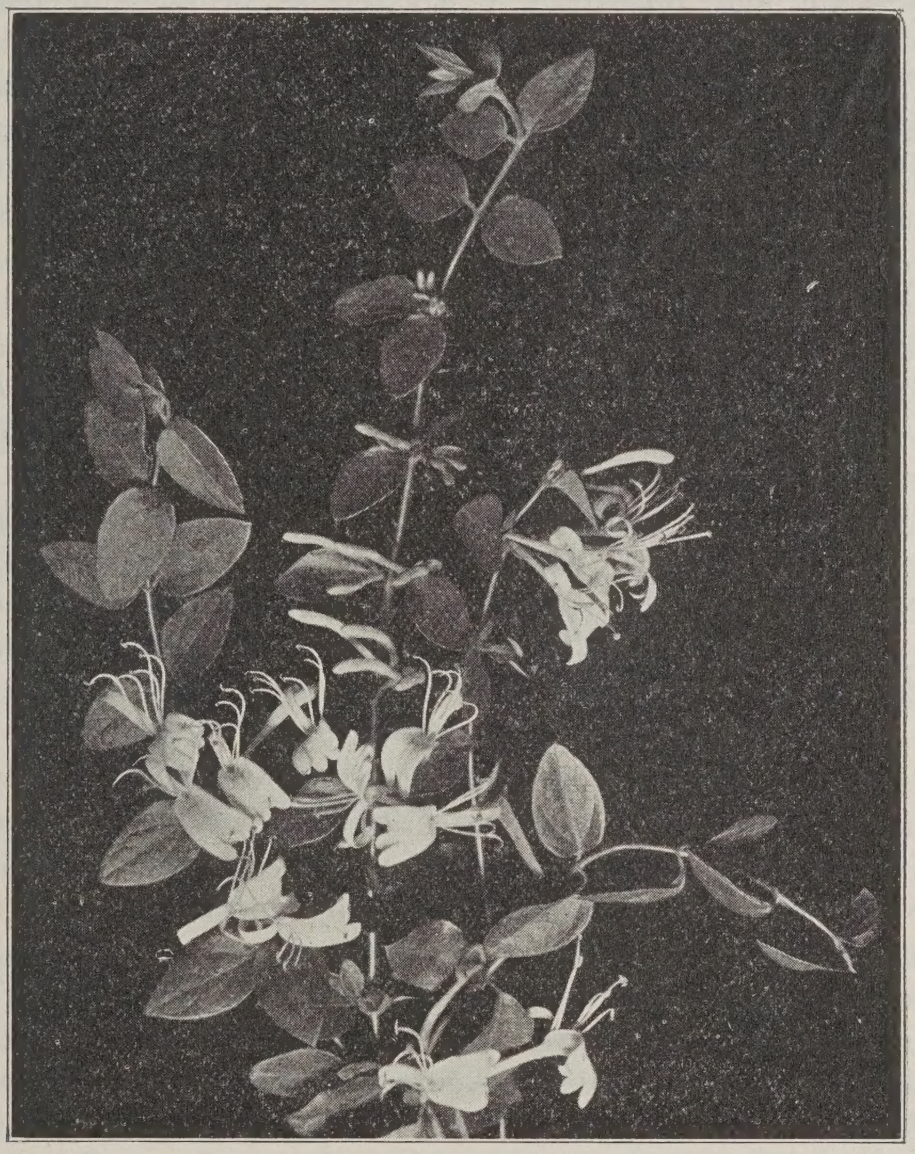


FIG. 536.—Japanese Honeysuckle (*Lonicera japonica*).

The petiolate leaves of *Cinchona* are opposite, with entire margins; the flowers (Fig. 535) resemble those of the Partridge Berry, but with the parts in 5s (as in *Coffea*), the two locules of the ovary with many ovules, and the fruit a dry, septicidal

[1] Different alkaloids (*e.g.*, quinine, quinidine, cinchonine, and cinchonidine) are obtained from the various species of *Cinchona*.

capsule. The seeds, with endosperm, are winged. The plant is cultivated by seeds, by cuttings, and by layering. While the red-bark becomes a large tree, the brown-bark becomes only a small tree, and the yellow-bark only a small tree or bush.

Gardenia and *Bouvardia*, cultivated as ornamental plants, also belong to the Rubiaceae.

The Honeysuckle Family (*Caprifoliaceae*) contains the Honeysuckles (*Lonicera*) (Fig. 536), Bush Honeysuckle (*Diervilla*, *Weigela*), Snowberry (*Symphoricarpos*), Twin-flower (*Linnaea* named from Linnaeus), the Viburnums, and the Elder (*Sambucus*). This family is not sharply distinguished by botanical features from the Rubiaceae. The shrubs and vines above mentioned are among our most prized ornamental woody plants.

The Valerian and the Teasel Families (*Valerianaceae* and *Dipsaccaeae*) are classed by some authors with the Rubiales, and by others in a separate order—the *Valerianales*.

The Valerian Family (*Valerianaceae*) includes the garden Valerian (*V. officinalis*), found along roadsides as a garden escape in New York and New Jersey. The plant was introduced in Europe and Asia and its roots and juice are officinal. *Valeriana edulis* (edible valerian) grows in moist situations on the prairies and plains from Ontario and Ohio westward to Minnesota and Iowa and beyond. It is sometimes cultivated over a wider territory. Garden Heliotrope (*Valeriana officinalis*), also a native of Europe and Asia, is found as an escape from cultivation in New England, New York, New Jersey, and Ohio.

In the Teasel Family (*Dipsacaceae*) the only species of economic importance is the Fuller's Teasel (*Dipsacus fullonum*). This plant comes originally from the Mediterranean region, and its dried heads (in fruit) have hooked paleae which make it valuable in fulling (*i.e.*, raising a nap on) woolencloth. The pieces of these paleae, remaining in the cloth, often make woolen underwear irritating to the skin.

ORDER, Cucurbitales

This order includes only the economically important Gourd Family (Cucurbitaceae).

GOURD FAMILY

The Gourd Family (*Cucurbitaceae*) comprises mainly herbaceous vines, all of which have tendrils (Fig. 537). The plants (Fig. 538) are monoecious or dioecious, and the 5-lobed calyx tube is adnate to the ovary. The five petals are inserted on the limb of the calyx, and are either separate or united in a sympetalous corolla. The one- to three-celled ovary ripens into a pepo or gourd. The possession of staminate and pistillate flowers has led to the saying, common among farmers of certain sections, that

FIG. 537.—Portion of vine of cucumber (*Cucumis sativus*), *t*, tendrils; *p*, ovary of pistillate flower; *s*, staminate flower.

"you must have a cucumber to start with or you can't get a cucumber," referring to the presence of the ovary in the flower stage. There are approximately 650 species grouped in about 90 genera mostly native in the tropics.

The family takes its name from the genus *Cucurbita*, with about ten species chiefly native in America, Asia and Africa. The Gourd (*C. Pepo*, var. *ovifera*), Scallop, Pumpkin, and Summer Crooknecked squashes and Vegetable Marrow are all cultivated varieties of *Cucurbita Pepo;* the winter and Canada Crookneck squashes are forms of *Cucurbita moschata.* Hubbard and Turban

squashes are forms of *Cucurbita maxima;* Cantaloupes, Muskmelons, and Honeydew melons are all derived from *Cucumis melo,* the Cucumber from *Cucumis sativus,* Gherkins from *C. anguria,* and Watermelon and Citron from *Citrullus vulgaris.* The term muskmelon is commonly restricted to the "nutmeg" melon, with a soft rind and netted markings on the surface. The cantaloupes are the warty, hard-rinded forms, common in Europe but not in America, where the word "cantaloupe" is a trade name, commonly applied to muskmelons.

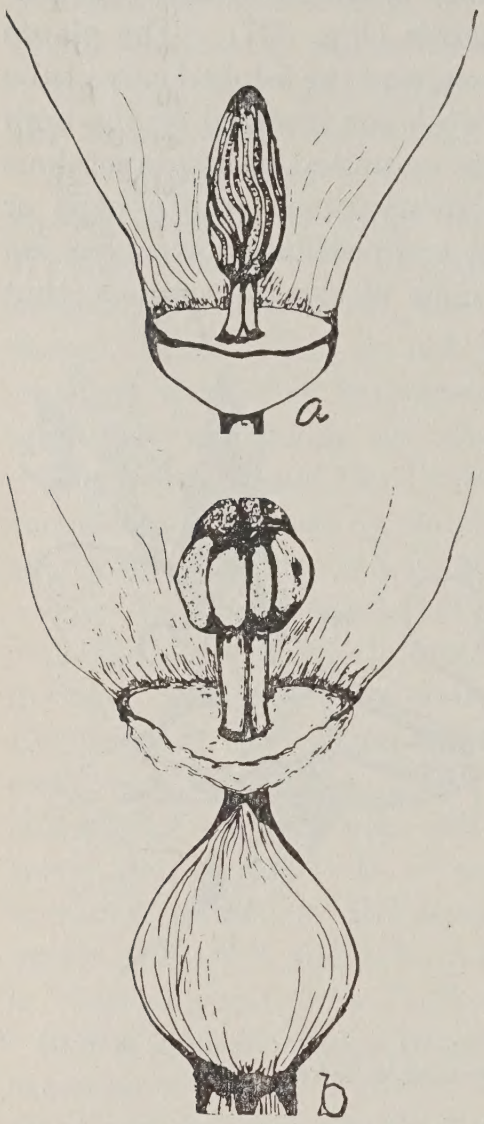


FIG. 538.—Structure of the flower of the squash (*Cucurbita Pepo* var.). *a,* vertical view of staminate flower, showing anthers ready to dehisce; *b,* pistillate flower, showing the knobs of the stigma, connected by the style with the ovary below. A portion of the sympetalous corolla has been removed in each case. (After Cummings and Stone. Vermont Agr. Exp. Sta.)

The form, *Citrullus vulgaris,* known as "citron" and used as an ingredient in pickles, is not to be confused with the commercial candied "citron," derived from *Citrus medica,* of the Rue family (Rutaceae, p. 651).

In Pumpkins (*Cucurbita Pepo*), Summer Crooknecks (*C. Pepo condensa*), Gourds (*C. Pepo ovifera*), and Winter Crooknecks (*C. moschata*) the fruit stalks are strongly ridged and the leaves are lobed; in the Hubbard squash the leaves (except occasionally on young shoots) are not lobed, and the fruit stalk is not lobed.

In the Turban Squash (*C. maxima*), which looks like one squash growing within another, the inner part is the ripened ovary, and the outer part is the receptacle which has thickened and grown up around the ovary (Fig. 539).

The botanical and historical evidence points to America as the home of the pumpkin. At the time of the discovery of America both pumpkins and squashes were being grown by the Indians, generally in fields of maize, as yellow pumpkins are grown now in certain regions. In 1913 and again in 1917 Small[1] found growing on the shore of Lake Okechobee, in Florida, a gourd-bearing vine, the foliage and flowers of which cannot be distinguished from those of the cultivated pumpkin. The fruits appear as

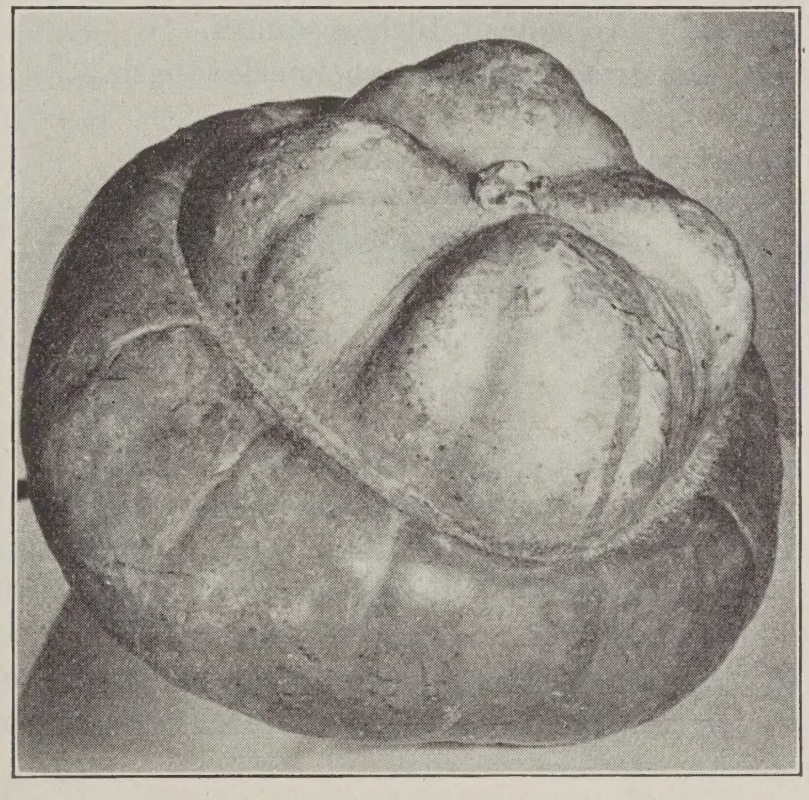


FIG. 539.—Turban squash (*C. maxima*).

diminutive pumpkins, and Small says: "There seems to be no good reason, therefore, for doubting that we really have discovered the pumpkin's Garden of Eden . . . The pioneer white men found the Seminole Indians of the peninsula cultivating a kind of pumpkin. This was popularly named the Seminole-pumpkin . . . It is possible that the pumpkins found by the early travelers and pioneer settlers in more temperate North America, as a staple cultivated crop among the American

[1] Small, John K. Wild Pumpkins. Jour. New York Bot. Gard. **23**: 19–23. Feb., 1922.

Indians, were descended from our wild Okechobee pumpkin, through the Seminole pumpkin as its more or less similar ancestor."

In tabular form the various cultivated forms are referred to the following genera, species, and varieties:

CUCURBITA

Pepo: pumpkin, summer crookneck squash, vegetable marrow, scallop.

Var. *ovifera,* "gourds."

maxima: Hubbard squash, turban squash.

moschata: winter and Canada crookneck squash.

CUCUMIS

Melo: muskmelons.

var. *reticulatus:* muskmelons (nutmeg or netted melon).

var. *cantalupensis:* cantaloupe or rock melon.

var. *culta:* mango melon.

sativus: cucumber.

anguria: gherkins.

CITRULLUS

vulgaris: watermelon, pickle "citron."

The evidence indicates that the muskmelons came from tropical Asia, and the cucumber from southern Asia. The cucumber has probably been cultivated in India for upwards of 3000 years. The "Sikkim cucumber" (*Cucumis Hardwickii* Rayle), from the Sikkin Himalayas, so closely resembles our cultivated cucumber in leaves, flowers, and fruits, that it is regarded as its probable wild progenitor.

Evidence as to the origin of the watermelon is somewhat conflicting. Early students of the problem regarded Africa as its native home, while Carrier[1] has recently adduced evidence that its native country is America.

Germination of Squash Seed.—The mode of germination of the squash seed is so unusual and interesting as to merit description. As the embryo begins to increase in size, a characteristic "peg" develops very rapidly (within about 24 hours) on the underside of the embryo-axis. This peg catches against the seed coat as the embryo grows and holds it down while the elongating arched hypocotyl pulls the cotyledons out of the coat (Fig. 540).

[1] Carrier, Lyman. The beginnings of agriculture in America. New York, 1923.

Charles Darwin showed that this peg develops at the zone where stem and root unite, and that the morphologically lower side of the peg is root-tissue and the morphologically upper side stem-tissue.[1] Darwin also noted that the peg always develops on the side of the axis which becomes concave by the arching of the hypocotyl, and his son, Francis Darwin, later inferred that the peg develops in direct response to the stimulus of gravity, for if a seed is rotated slowly on an instrument called a *clinostat* so that the axis of the horizontally placed hypocotyl coincides with the axis of rotation, then all sides of the hypocotyl are equally exposed to the action of gravity, and the peg develops, not as an organ on one side, but (with exceptions) as a projecting ring of tissue

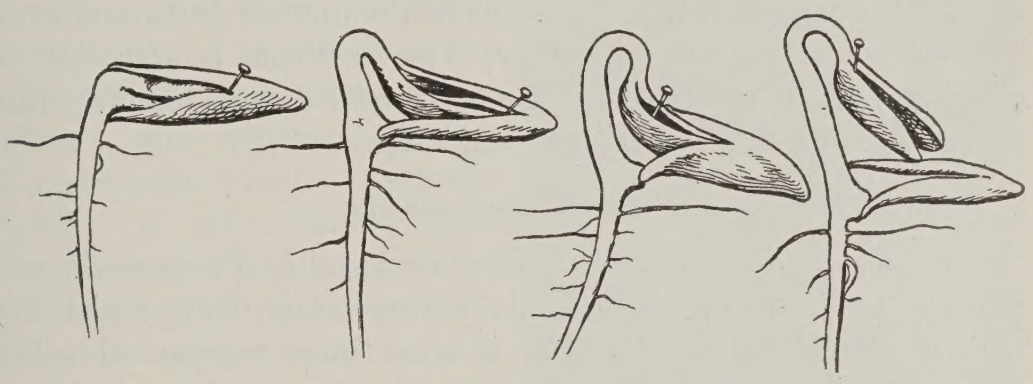


FIG. 540.—Germinating seeds of a squash, showing the method by which the "peg" functions in the removal of the seed-coat. (Redrawn from Crocker, Knight, and Roberts.)

extending around the hypocotyl. Later, and more detailed experiments,[2] however, indicate that the peg is a natural organ of the plant, developing on all sides of the hypocotyl if arching of the latter is avoided. Its location on one side of the hypoctyl is apparently to be attributed to the arching of the hypocotyl, and the arching, in turn, is brought about by the action of two stimuli, namely, gravity and the contact of the hypocotyl with the seed

[1] Root hairs were found on the lower side but not on the upper, and the color-reaction of the two sides to potassium permanganate afforded confirmatory evidence. Darwin showed that when very young seedlings are immersed in this reagent the tissue belonging morphologically to the stem does not stain, while the radicle or root-tissue stains brown. Darwin also found that, in some cases, secondary roots spring from the lower surface of the peg.

[2] Crocker, Knight, and Roberts. The peg of the Cucurbitaceae. Bot. Gaz. **50**: 321–339. Nov., 1910.

coats. Gravity, therefore, acts only indirectly as a stimulus to the formation of the peg, and is only one of at least two known factors.

The Chayote,[1] another plant of the Gourd Family, has been cultivated since very ancient times in Central America, later in Mexico and the West Indies, and more recently in some of the southern United States. The vine has a perennial root which bears large edible tubers in subtropical regions (*Cf.* p. 103) and also edible fruits in great quantity The plant is interesting, botanically because its seed, like that of the mangrove (p. 702), apparently has no resting period. But, in contrast to the mangrove, the tip, only, of the hypocotyl (by the growth of the cotyledons) emerges from the apex of the mature fruit, and from the tip several roots develop. The seed coat largely fails to develop, so that the tissue of the fruit itself serves, like an endosperm, to nourish the young growing embryo.

ORDER, Campanulales

This order includes the Bellflower Family (*Campanulaceae*) and the great Composite Family (*Compositae*), from which the Chicory Family (*Cichoriaceae*) is sometimes segregated. The name of the order refers to the bell-shaped (campanulate) corolla. There are usually five stamens. The pistil has an inferior ovary and a two-cleft stigma.

BELLFLOWER FAMILY

The Bellflower Family (*Campanulaceae*) includes the cultivated perennial Harebell or Blue-Bells-of-Scotland (*Campanula rotundifolia*) and other cultivated bell-flowers (Fig. 541). The Blue-Bells-of-Scotland are found wild, not only in Scotland, but throughout northern Europe and Asia and from Labrador westward to Alaska, and south to New Jersey, Nebraska, and California. There are at least 50 other species in the genus, mostly perennial, but some biennial and some annual. The well-known Canterbury Bells (*Campanula Medium*) is a biennial, and *C. Erinus*, a Mediterranean species used in rock gardens and edgings, is an annual.

Here, also, belongs *Lobelia*, named after Matthias de l'Obel, or Lobelius (1538–1616), a Flemish botanist, famous as the author

[1] Chayote, pronounced *chī-ō′-tĭ*.

of one of the well known herbals. The bright scarlet or red flowers of *Lobelia cardinalis* (the Cardinal Flower) are conspicuous autumn flowers along streams, and Indian Tobacco (*L. inflata*) is officinal. Other species are cultivated for the beauty of their flowers. By some botanists *Lobelia* is classed in a separate family, the *Lobeliaceae*.

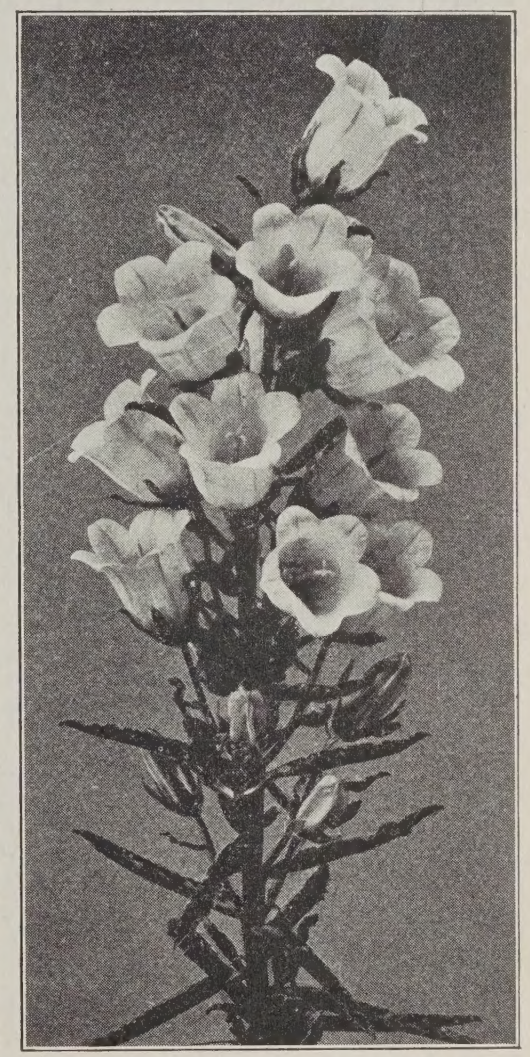


FIG. 541.—Bellflower (*Campanula* sp.).

COMPOSITE FAMILY

The Composite Family (*Compositae*) is the largest of the plant kingdom. In all the species the flowers are in heads and have *syngenesious* anthers (*i.e.*, united in a tube). The chicories and ragweeds are segregated by some authors into separate families (Cichoriaceae and Ambrosiaceae). If we include those two groups in the Compositae we have nearly 1000 genera and considerably over 10,000 species. Notwithstanding its large size the family is of comparatively slight economic importance so far as its cultivated forms are concerned, although it includes some of our most troublesome weeds. In the Cichoriaceae most of the forms have a milky, bitter juice, and the individual florets of the head have a strap-shaped (ligulate) corolla. From the latter feature the group is sometimes called the *Liguliflorae*.

Cichorium Intybus, commonly known as *Chicory* or Succory Fig. 542), is conspicuous in fields, roadsides, and waste places from July to October with its striking blue flowers. The ground, roasted roots of this plant afford one of the chief adulterants of coffee. It is also used as a salad and as fodder. The plant is common in the continental old world. Other

economic plants of this group are the Oyster Plant or Salsify (*Tragopogon porrifolius*), Endive (*Cichorium Endivia*), and Lettuce (*Lactuca sativa*). Endive is common in the regions bordering the Mediterranean.

The cultivated lettuce is closely related to the wild *L. Scariola*, from which it may have been derived. Crosses have been made

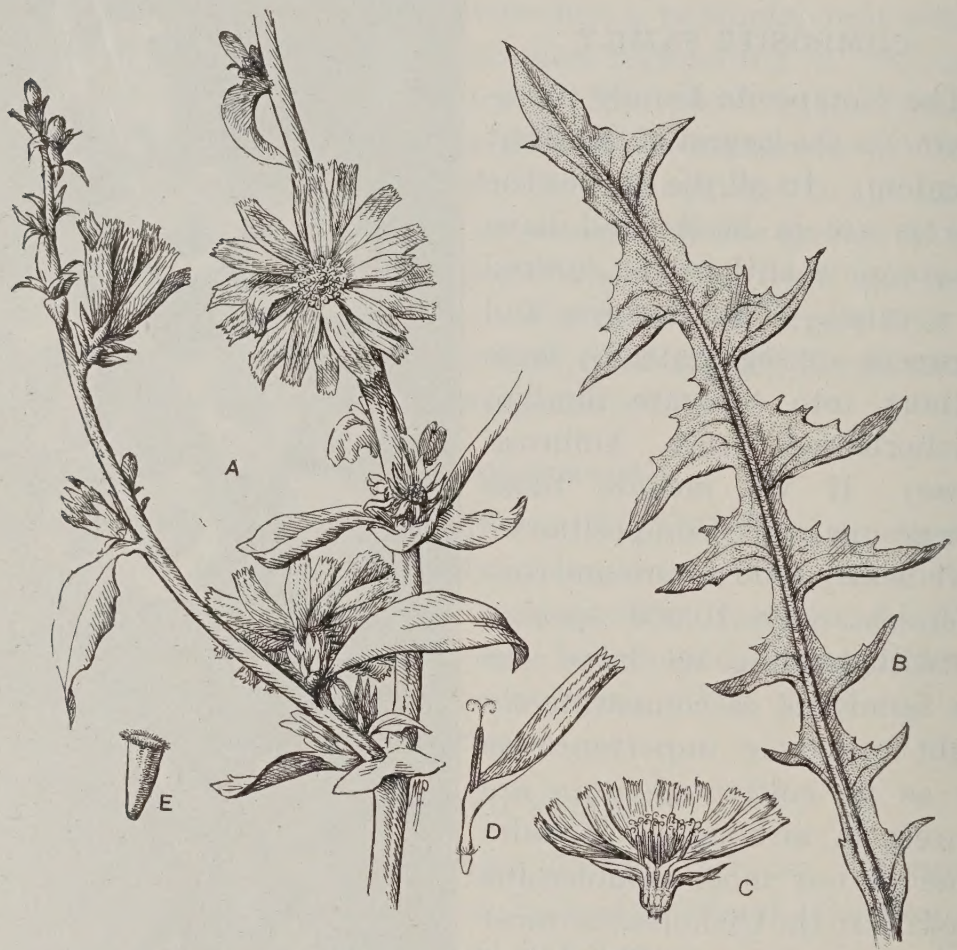


FIG. 542.—Chicory (*Cichorium Intybus*). *A*, portion of flowering branch; *B*, basal leaf (runcinate-pinnatifid); *C*, median longitudinal section through a head, showing the insertion of the flowers; *D*, individual flower; *E*, fruit (ripened ovary), showing the persistent pappus (calyx) of short scales.

between the wild and cultivated forms. It has been cultivated for more than 2000 years, and there are more than 100 horticultural varieties (Fig. 662). Lettuce formed a part of the diet of the kings of Persia 300 years before Christ. As noted on page 112, the leaves of the wild *L. Scariola* are very sensitive to light, and tend to orient themselves in a north-south plane (Fig. 77). For this reason the plant is often called the compass-plant. The Hawkweed or "Devil's Paint Brush" (*Hieracium aurantiacum*),

and other species of *Hieracium* are fast becoming the most troublesome weeds of the meadows in the eastern United States.

Among the Ambrosiaceae the Ragweeds, especially the Great Ragweed (*Ambrosia trifida*) (Fig. 543) and Roman Wormwood (*A. artemisiifolia*) are, through the abundance of their wind-borne pollen, one of the chief causes of bronchial *asthma*. (*Cf.*, p. 401.)

FIG. 543.—Great Ragweed (*Ambrosia trifida*).

The *Compositae* proper have ligulate ray florets and companulate (bell-shaped) disc florets. The group includes the well known White Daisy or Whiteweed,[1] (*Chrysanthemum Leucanthemum;* or its cultivated form, the Marguerite; Boneset or Thoroughwort (*Eupatorium perfoliatum*), and its close neighbor and near relative Joe-Pye-Weed (*E. purpureum*); the Golden-rods (*Solidago*), with about 100 species, nearly 50 of which are found in the eastern United States; and the Asters (*Aster*), with nearly 250 species, of which about 150 occur in North America; the Yellow Daisy (Cone-flower, Black-eyed Susan, *Rudbeckia hirta*); the Sunflowers (*Helianthus* sp.), including the Jerusalem Artichoke (*Helianthus tuberosus*); *Coreopsis* (wild and cultivated) (Fig. 544), the troublesome Sticktights (*Bidens* sp.); *Gailardai* (wild and cultivated); Camomile (*Athemis*); Tansy (*Tanacetum vulgare*); Burdocks (*Arctium*) (Fig. 545); Thistle (*Carduus*); Centaurea (wild and cultivated); and the ubiquitous Dandelion (*Taraxacum* sp.).

[1] The white "daisy" of the United States is not to be confused with the European daisy, *Bellis perennis*.

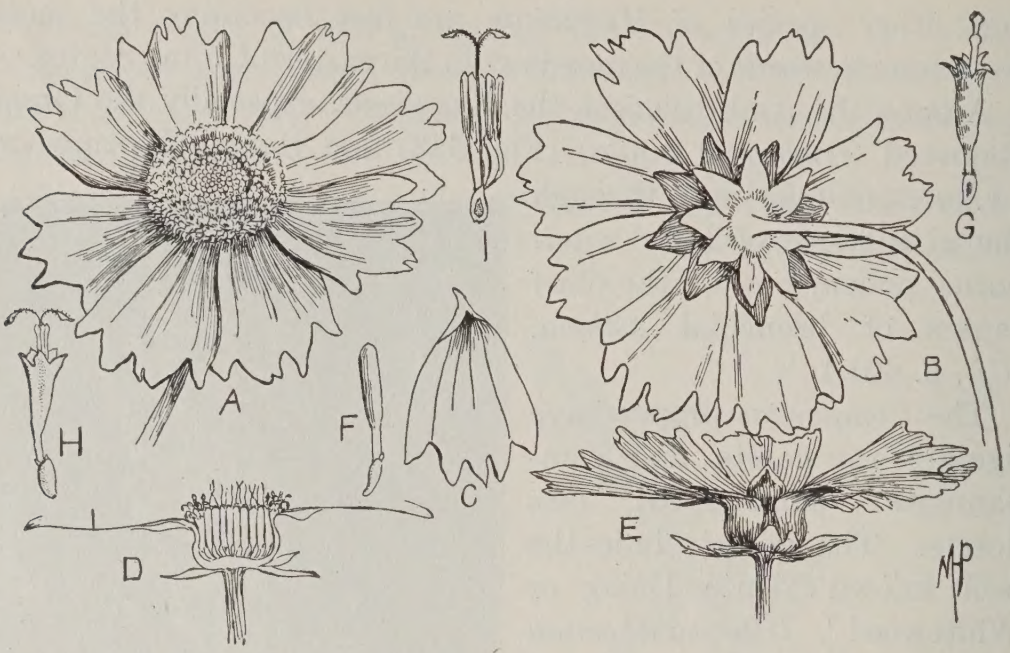


FIG. 544.—A composite (*Coreopsis* sp.). *A*, *B*, *E*, views of the inflorescence or head; *C*, a ray-flower; *D*, section through the head; *F*, a disc-flower in bud; *G*, disc-flower just opened; *H*, older disc-flower, the stigmas reflexed; *I*, disc-flower with corolla removed.

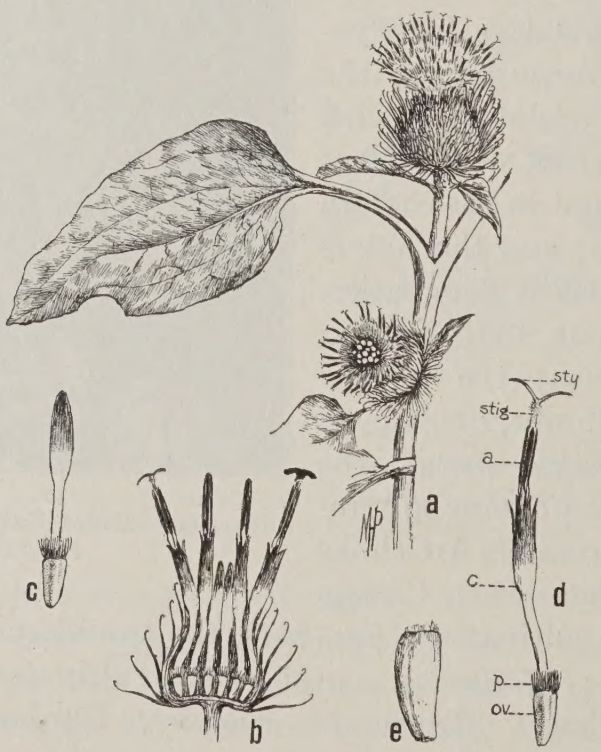


FIG. 545.—Inflorescence and flowers of the burdock (*Arctium minus*). *a*, Inflorescences; *b*, longitudinal section of the same; *c*, bud of individual flower; *d*, mature flower; *sty*, stigma; *stig*, style; *a*, ring of syngenesious anthers; *c*, corolla; *p*, pappus (calyx); *ov*, ovary; *e*, mature seed.

CHAPTER XXXVI

MONOCOTYLEDONS

The monocotyledons were at one time considered more primitively organized than the dicotyledons, and they were consequently placed before them in the manuals. More recent studies of the embryogeny of the angiosperms, however, have resulted in evidence that the dicotyledons are the more primitive, and that the monocotyledons were derived from them by a process of simplification.

In the development of the angiosperm embryo there is formed on the axis near the apex of the embryonic stem (hypocotyl) a "cotyledonary ring." As the embryo matures, the growth of this ring becomes localized at one or more points; when growth proceeds at several points we have a polycotyledonous embryo, as in the pines; when growth is confined to two points, 180° apart we have a dicotyledonous embryo, as in the bean, cotton, potato, rose, and all the groups of plants known as dicotyledons; when growth is wholly or largely (and normally) confined to one region or growing point we have a monocotyledonous embryo as in wheat, corn, lily, and the entire group of monocotyledons. In the latter case the cotyledon *appears* to be terminal. Of course there are other anatomical characters commonly correlated with the possession of one or of two cotyledons, such as parallel veined leaves and endogenous stem with one cotyledon, and netted veined leaves and exogenous growth with two cotyledons, as noted more in detail on pages 354–356. There are, however, a number of exceptions to this. The flower structure is also unlike in the two groups, the parts being normally in threes in the monocotyledons, but usually in fives or fours in the dicotyledons. In the Magnolia group (Ranales) of the dicotyledons the parts of the flower are frequently in threes (*e.g.*, *Anonaceae* and *Magnoliaceae*).

In some cases the number of cotyledons formed is abnormal to the group; thus, dicotyledonous plants may at times produce

seeds with three cotyledons (not uncommon, for example, with beans, or with maple seeds) (Fig. 546), or one of the growing points

FIG. 546.—Polycotyledonous seedlings of dicotyledonous species. *a–c*, *Silene odontipetala*, with hemi-tricotylous, tricotylous, and tetracotylous seedlings; *d–h*, *Papaver Rhoeas* (semi-double cultivated form), dicotylous, hemi-tricotylous, tricotylous, tetracotylous, and pentacotylous seedlings; *i*, *Acer Pseudo-Platanus*, tetracotylous seedling. (All figures redrawn from de Vries.)

on the cotyledonary ring may early cease its development. In certain dicotyledonary groups this latter is the normal character, giving rise to a so-called *monocotyledonous dicotyledon*, such as the Water Chestnut (*Trapa natans*), Butterworts (*Pinguicula* sp.), and others (Fig. 250). On the other hand, plants that are normally monocotyledonous may develop a rudimentary second cotyledon. This is normally the case with many of the cereals, where the (more or less) rudimentary second cotyledon forms the so-called *epiblast*. In some of the grass family the epiblast is regularly almost as large as the other cotyledon. In the liliaceous South African plant, *Agapanthus umbellatus*, embryos are sometimes found with two fully developed cotyledons (Fig. 547), and in certain other monocotyledons the embryo has normally two distinct cotyledons, giving rise to the so-called *dicotyledonous monocotyledons*, as in the Black Bryony (*Tamus communis*) and *Dioscorea bonariensis*, of the Yam Family (Fig. 250), and various grasses (Fig. 251).

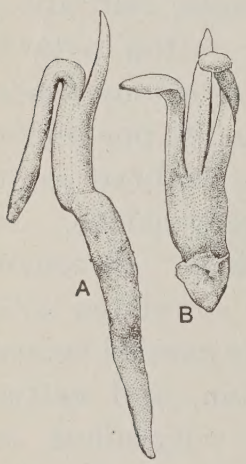


FIG. 547.—*Agapanthus umbellatus*. *A*, monocotyledonous embryo. *B*, dicotyledonous embryo. (Redrawn from photo by W. J. G. Land.)

In these cases of abnormal number of cotyledons the other structural features (of stem, leaf, and flower) commonly retain the distinctive characteristics of the group, so that it is not difficult to assign the plant to its proper sub-class. Often abnormality in

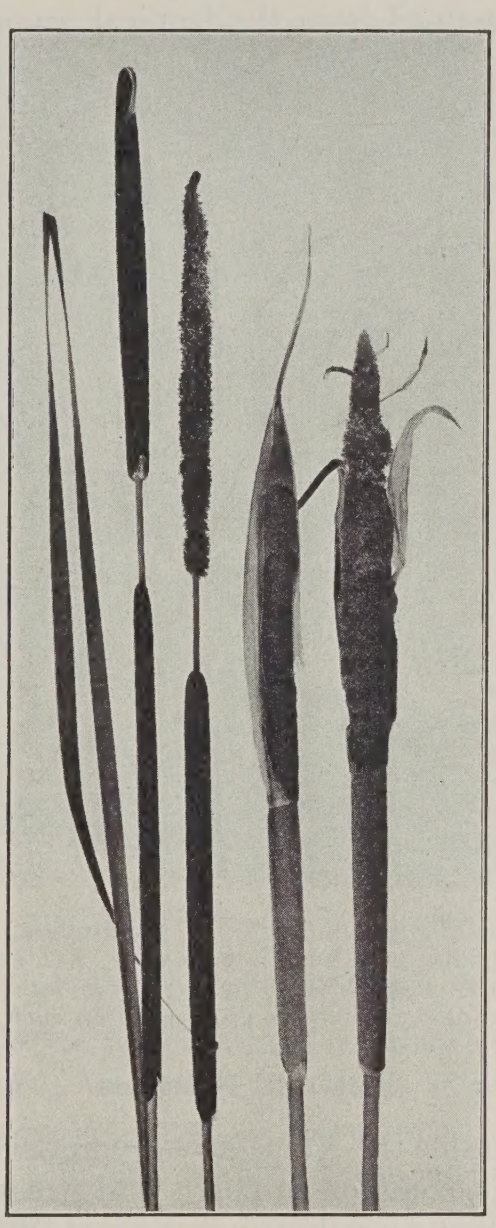


FIG. 548.—Cat-tails. *Typha angustifolia* at left; *Typha latifolia* at right. Staminate flowers above; pistillate flowers below.

the number of cotyledons appears to be an expression of environmental influence. However, a careful study of all the evidence has led to the conclusion that the monocotyledons have been derived from the dicotyledons; they are, therefore, a later group.

As to what are the most primitive monocotyledons is a disputed question. Here the ordinary sequence of the manuals is followed.

ORDER, **Pandanales**

This order is named from the tropical genus, *Pandanus*—the so-called "screw pine," whose fibers are used in making fiber hats. Here belong the Cat-tail Family (*Typhaceae*) (Figs. 548 and 549), and the Bur-reeds (*Sparganiaceae*).

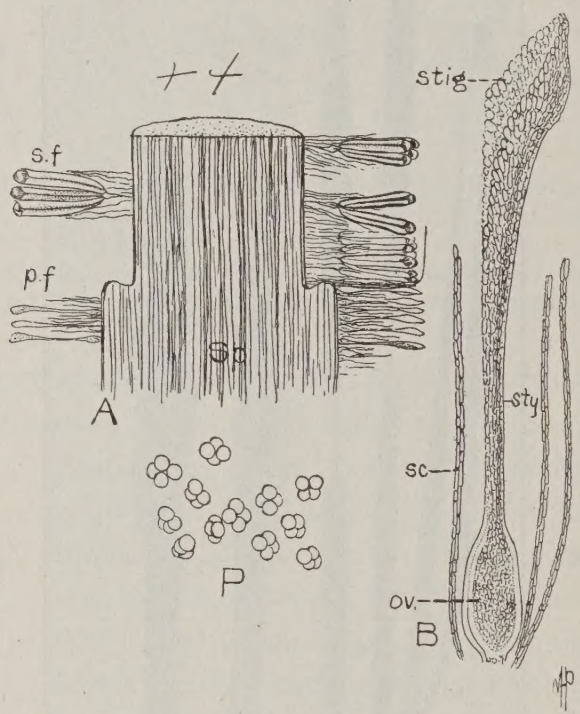


FIG. 549.—Cat-tail (*Typha latifolia*). *A*, longitudinal section of portion of inflorescence; *Sp*, spadix; *p.f.*, pistillate flowers; *s.f.*, staminate flowers. *B*, pistillate flower, greatly magnified; *ov*, ovary; *sty*, style; *stig.*, stigma; sc, sterile hair; *P*, pollen grains, in characteristic groups of four each. (Cf. Fig. 375.)

ORDER, **Naiadales**

This order contains the *Naiadaceae*, comprising the Pondweeds (*Potamogeton* sp.), common in ponds and streams of the old and the new worlds, and several other genera of little or no economic importance; the Arrowgrass Family (*Scheuchzeriaceae*); the Water-Plantain Family (*Alismaceae*), comprising the well known Water-Plantain (*Alisma Plantago-aquatica*) (Fig. 550), the Arrowheads (*Sagittaria* sp.), and other genera of no economic significance; and the Tape-Grass Family (*Vallisneriaceae*), containing the well known Eel-grass (*Vallisneria spiralis*) of the streams and

ponds of the old and new world (Fig. 361), the Water-Weed (*Elodea* or *Philotria*), common in fresh water aquaria, and the Frog's bit (*Limnobium*). Neither the Pandanales nor the Naiadales contain species of more than minor economic importance.

FIG. 550.—Water-Plantain (*Alisma Plantago-aquatica*).

ORDER, **Graminales**

This order, with two families, the Gramineae (grasses) and the Cyperaceae (sedges), contains the most important economic plants of the monocotyledons, and some of the most, if not the most, important economic plants of the ancient and modern world, including the cereals of the Grass Family. Some of the grasses are troublesome weeds, *e.g*, Barnyard grass (*Echinochloa*), Foxtail grass (*Setaria*), Quick, or Couch grass (*Agropyron*) with long creeping rhizomes, Johnson grass (*Sorghum halepense*) (Fig. 551), and numerous others.

The flowers of grasses and sedges never have sepals and petals but, instead, scale-like bracts or glumes which enclose one or

more flowers. The flowers and enclosing bracts, with the short stem to which they are attached, comprise the *spikelet*, the unit of the grass inflorescence (Fig. 566).

GRASS FAMILY

The plants of the Grass Family (*Gramineae*, or *Poaceae*) are mostly annual or perennial herbs, though a few have a tree-like or shrub-like habit, such, for example, as the Small Cane (*Panicum latifolium*) of our Southern States, and the Sugar Cane (Fig. 578). Of approximately 1500 species of grasses in the United States, about 60 are cultivated, and about the same number are troublesome weeds introduced from Europe and other foreign countries.

FIG. 551.—Johnson-grass (*Sorghum halepense*). Spikelets in a panicle. (After Britton and Brown.)

The leaves of grasses have three, more or less clearly differentiated, parts, namely, the *base*, the *blade*, and the *ligule* (Figs. 552 and 553). The leaf-base is developed into a long *sheath*, which surrounds the internode and thus gives support to the stem. This is specially important in grasses and other Monocotyledons whose internodes have a long period of elongation due to intercalary growth of their tissue. In Dicotyledons the leaf-base, which is usually not developed into a sheath, serves as a protection to axillary buds, sometimes, as in the Plane tree (*Platanus*), growing over the bud like a cap. In Grasses, bud protection, as Goebel pointed out, is afforded by the ligule, which is a membranous growth at the base of the blade. It has also been thought that, in some cases, the ligule acts advantageously to the plant in preventing rain water from running down from the blade between the sheath and the stem.

The inflorescence of grasses is either a *spike* (Fig. 554) or a *panicle* (Fig. 551). When the spikelets are sessile, or nearly so, on the main axis of the inflorescence, a spike results, as in Quick grass (*Agropyron repens*), Crab grass (*Digitaria*), Gama grass (*Tripsacum dactyloides*), and others. When the main axis is divided and the spikelets are borne on the branches, a panicle

results, as in Orchard grass (*Dactylis glomerata*), Blue grass (*Poa pratensis*), all species of Panic grass (*Panicum*), Johnson grass, and others. The inflorescence of Timothy (*Phleum pratense*) is a spike-like, false panicle (Fig. 567).

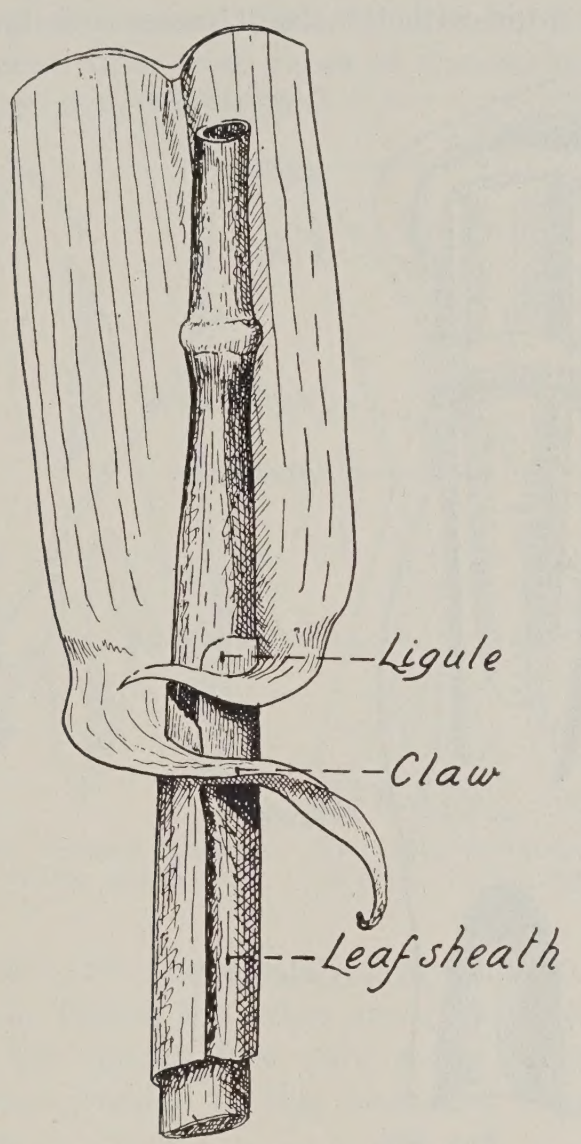


FIG. 552.—Portion of stem and leaf of Barley (*Hordeum*), showing the leaf-sheath, and the basal part of the blade with its ligule and claws. (After F. E. Lloyd.)

The two lower scales (and sometimes the upper scale) do not usually subtend flowers. The flowering glume, called a *lemma*, is often awned. Opposite the lemma is another scale, the *palet* or *palea*,[1] commonly awnless. In some grasses the palet is minute

[1] *Palea* is the Latin word for chaff.

or lacking, as in the Bent Grasses (*Agrostis*). At the base of the flower are commonly found two (sometimes three) small, thin scales, the *lodicules*. These are lacking in some species.

Sedges (*Cyperaceae*) and Rushes (*Juncaceae*) are often confused in the popular mind with the true Grasses. Sedges may be dis-

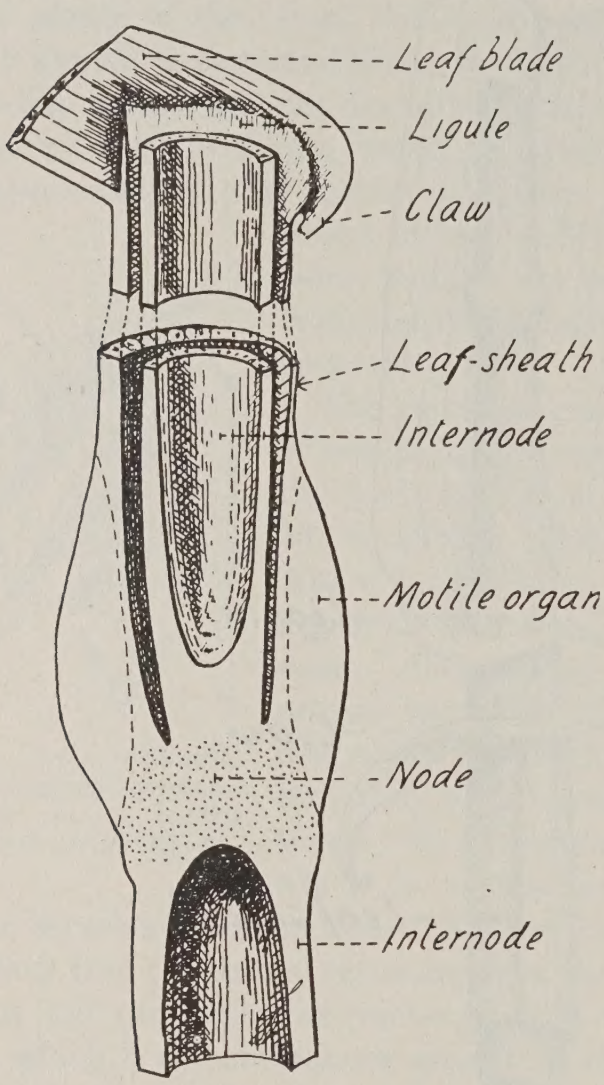


FIG. 553.

FIG. 554.

FIG. 553.—Longitudinal sections through a node of wheat straw. The broken lines indicate the shape of the leaf-base (false node) when dry and shrunken. (After Lloyd.)

FIG. 554.—*Tragus racemosus*. Terminal spike with one-flowered spikelets. (After Britton and Brown.)

tinguished from Grasses by the fact that their leaves are in three vertical rows (3-ranked) on a usually solid stem or *culm*, whereas the leaves of Grasses are 2-ranked on a hollow stem. Sedge culms are also commonly 3-sided, but those of grasses are

never so. In the inflorescence of Sedges (Fig. 555) there is no bract or palet between the flower and the rachilla. The perianth is of bristles or scales, rarely calyx-like, sometimes wanting. The fruit of the true grasses is a caryopsis (grain), while the fruit of the sedges is an achene and that of the rushes a capsule. The flowers of Rushes differ from those of Grasses in having a six-parted, green perianth (Fig. 556).

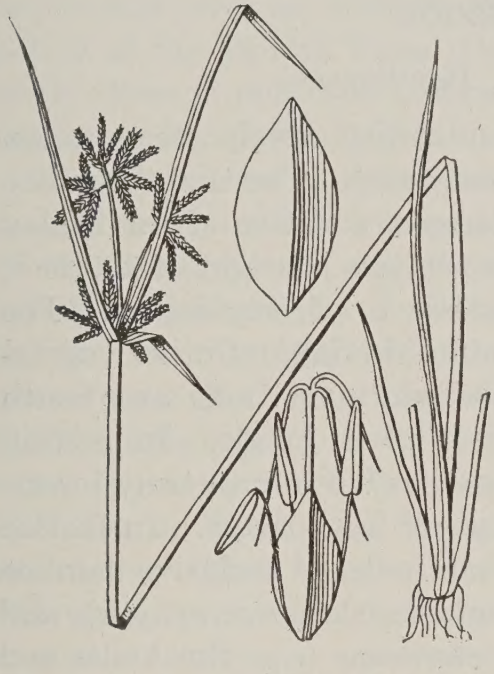


FIG. 555.—Brown Cyperus (*Cyperus fuscus*). (After Britton and Brown.)

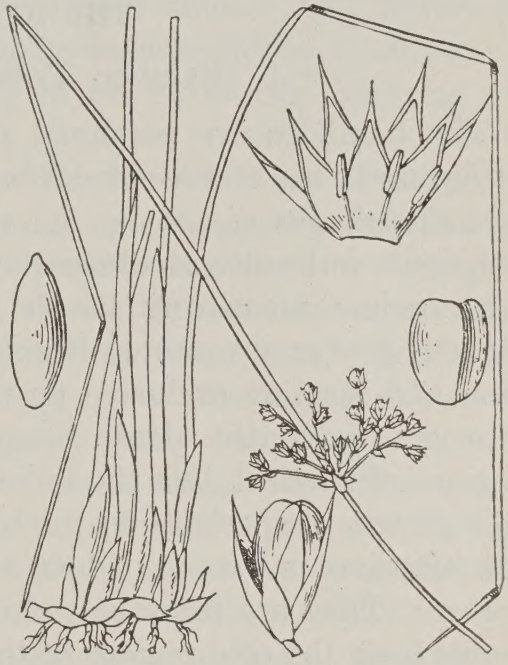


FIG. 556.—Common Rush (*Juncus effusus*). (After Britton and Brown.)

Classification.—The Grass Family is divided into Sub-Families, these again into Tribes, the tribes into Genera, the genera into Species, and the species into cultivated Varieties. For the cultivated genera treated in this book the classification is as follows:[1]

Subdivisions of the Gramineae

Sub-Family 1, Poateae

Tribes

1. Bambuseae (*e.g.*, Bamboos)
2. Hordeae (*e.g.*, Wheat, Rye, Barley)

[1] Following Hitchcock, A. S. The genera of grasses in the United States. U. S. D. A. Bull. 772. Washington, 1920.

3. Aveneae (*e.g.*, Oats)
4. Agrostideae (*e.g.*, Timothy)
5. Orizeae (*e.g.*, Rice)

Sub-Family 2, Panicateae

6. Paniceae (*e.g.*, Foxtail Millet)
7. Andropogoneae (*e.g.*, the Sorghums)
8. Tripsaceae (*e.g.*, Indian Corn)

THE BAMBOOS

(Bamboo Tribe, Bambuseae)

The bamboos are perennial plants with woody stems, often attaining to the stature of shrubs and trees. The Giant Bamboo (*Dendrocalamus giganteus*), for example, a native of the Malay peninsula but cultivated elsewhere, attains a height of 120 feet, with culms measuring 25–30 inches in circumference. The various genera are rank growers, often driving out other vegetation and forming exclusive growths which, in India and South America, have the dense character of a jungle. In certain regions of tropical Asia the taller species often form truly forest-like growths, especially on the banks of large rivers. In British Burma there is a stand of 1800 square miles of exclusive bamboo forest. They are commonly drought-resistant (*xerophytic*), and range from the cold regions of the snow-line (*e.g.*, the Andes and Himalayas) to the warmest tropical climates.

The stems or culms spring from a perennial underground rhizome and, as in most grasses, are hollow, except at the joints or nodes, where the hollow is closed by a strong diaphragm. The leaf-blade is jointed at the base and is attached to the stem by a short petiole, in contrast to the sessile leaf, characteristic of most Grasses. Also in contrast to most Grasses, the flower has three lodicules and six stamens (instead of the two lodicules and three stamens common to Grasses). The spikelets have numerous flowers arranged in racemes or panicles according to the species.

Blooming.—Some species bloom each year, but others only at long intervals. Thus, *Bambusa arundinacea* (the Spiny Bamboo), which grows wild and cultivated in Burma, India, Java, and elsewhere, flowers only after an interval of (apparenly) exactly thirty two years, reproducing by seed at such long periods.

After flowering and fruiting the plants die when, as Watt graphically describes it, "A forest of surpassing splendour is transformed into one of desolation and death, soon followed by fire, until the charred stems, dust and ashes are all that remain." The area over which *gregarious flowering* occurs is often very extensive; thus the Male Bamboo (*Dendrocalamus strictus*) was reported by the Indian Forester in 1901 as having flowered almost universally over an area of 1200 square miles. The flowering period of the Talipot Palm (*Corypha umbraculifera*) is 40 years, while there is only one instance on record of the flowering of the liana, *Bauhinia anguina*.

This phenomenon of gregarious flowering has not been satisfactorily explained. It is common among the genera and species of the bamboos, and has been variously explained as brought about by drought, by depletion of nourishment, by injury, or as the manifestation of a hereditary character. *Bambusa arundinacea* (the Spiny Bamboo and one of the largest species), flowers gregariously about every 30 years (some writers say every 50 years), not only in India where annual droughts occur, but also in Buitenzorg, Java, where droughts are practically unknown. Other species are known to flower gregariously following a wet season. Seifriz,[1] after carefully considering the available evidence, concludes that the rhythmic, gregarious flowering of bamboos is due to a hereditary (germinal) factor, which may be somewhat influenced or modified by environmental conditions.[2]

Classification.—Hackel divides the bamboos into four "subtribes," with 23 genera, as follows:

1. *Arundinarieae*, with 3 stamens, a two-keeled palea, and the pericarp grown fast to the seed (that is, the fruit is a true caryopsis).

[1] Seifriz, William. Observations on the causes of the gregarious flowering in plants. Am. Jour. Bot. **10**: 93–112. 1923.

[2] The Pigeon Orchid (*Dendrobium crumenatum*) flowers *simultaneously* over considerable areas, but not rhythmically like the bamboos, for the flowering interval may vary from a few days to several months. Here a climatic factor (probably a copious rain), starts the flower buds which are of the same age and come into flower simultaneously eight days after receiving the external stimulus. (Seifriz, W. The gregarious flowering of the orchid, *Dendrobium crumenatum*. Am. Jour. Bot. **10**: 32–37. 1923.)

Genera: *Arundinaria*, *Phyllostachys*, and five others.

2. *Eubambuseae*, with 6 stamens, a two-keeled palea, fruit a caryopsis with a thin, delicate pericarp.

Genera: *Bambusa* and four others.

3. *Dendrocalameae*, with 6 stamens, a two-keeled palea, the pericarp forming a hard thick or fleshy shell free from the enclosed seed (fruit a nut or a berry).

Genera: *Dendrocalamus* and five others.

4. *Melocanneae*, with 6 to many stamens, palea not keeled and resembling the flowering glumes (and thus, by some, considered wanting), fruit berry-like, with a thick fleshy pericarp.

Genera: *Melocanna* and two others.

Uses.—The bamboos as a group are of outstanding economic importance, serving mankind in a multitude of ways in connection with almost every phase of life. In this respect they are comparable with the coconut and date palms. In India, eastern Asia, Japan, and the Malay Archipelago, the bamboos have become really indispensable. The stems are used for building houses and fences, boats and floats; the hollow stems are extensively used as water pipes and as buckets for carrying water and on fixed rotating wheels for dipping water into irrigation ditches. In certain countries of the "near East" practically all the furniture and innumerable household utensils, toilet articles, and ornaments, and many agricultural implements, are made of bamboo. It is largely the nodes that are used as containers; the internodes of certain species serve as beehives. Masts of boats, carrying poles, and palisades of defense are made of the larger stems. Among innumerable uses are also the following: wind instruments and instruments of percussion; aeolian harps (by perforating the stems and allowing the wind to blow through). From finely-split bamboos are made roofing, ropes, mats, baskets, hats and other objects. The Chinese umbrellas are of bamboo handles and ribs, covered with bamboo paper. "Of all the fibre-yielding plants known to botanical science, there is not one so well calculated to meet the pressing requirements of the paper-trade as 'Bamboo,' both as regards facility and economy of production, as well as the quality of the '*paper-stock*' which can be manufactured therefrom; grown under favorable conditions of climate and soil, there is no plant which will give so heavy

a crop of available fibre to the acre, and no plant which requires so little care for its cultivation and continuous production."[1]

FIG. 557.—Inflorescences of *a*, Oat (*Avena strigosa*), *b*, Wheat (*Triticum vulgare*), *c*, Rye (*Secale cereale*).

The leaves are used for filling mattresses, and the young tender bamboo shoots are eaten as a vegetable, like asparagus. A silicic acid secretion, known as Tabashir (Tabasheer), or Bamboo

[1] Routledge. On bamboo considered as a paper-making material. Cited by Watt, George. A dictionary of the economic products of India. **1**: 378. 1889.

Manna, collects in the hollow internodes of *Bambusa arundinacea* and a few other species. This substance is highly esteemed as a medicine by the Hindus and Mohammedans.

The seeds of various species are an important article of diet, and on several occasions during a period of famine, when the rice and other stable articles of food failed, bamboo seeds have saved the lives of tens of thousands who might otherwise have perished. The bamboo, says Wallace,[1] is one of nature's most valuable gifts to uncivilized man. The statement, in large measure, applies to civilized man as well.

FIG. 558.—Spikes of the types of wheat. 1, Polish (*T. polonicum*); 2, Club (*T. compactum*); 3, Common (*T. vulgare*); 4, Poulard (*T. turgidum*); 5, Durum (*T. durum*); 6, Spelt (*T. spelta*); 7, Emmer (*T. dicoccum*); 8, Einkorn (*T. monococcum*). (After Robbins.)

WHEAT

(Barley Tribe, Hordeae)

The Barley Tribe, including wheat, rye, barley, and other grains, differs from the following or Oat Tribe in having the inflorescence in spikes instead of in panicles (Fig. 557), and in having a straight awn at the end of the flowering glume, instead of a bent awn on the back of the glume.

[1] Wallace, A. R. The Malay Archipelago.

The Wheats belong to the genus, *Triticum*. By some authors this genus is made to include, as a section, the old genus *Aegilops*. The species and varieties of *Triticum* (following Hackel[1]) are as follows (See also Fig. 558):

Triticum	sativum	tenax	Vulgare Vill	Common wheat
			compactum Host	Club wheat
			turgidum L	Poulard wheat
			durum Desf	Durum wheat
		dicoccum Schr		Emmer
		spelta L		Spelt
	polonicum L			Polish wheat
	monococcum L			Einkorn

In contrast to Timothy grass, wheat is an annual having (in the latitude of the United States) two seasonal groups—namely, *winter wheat*, sown in the fall and harvested in early summer; and *spring wheat*, sown in the spring and harvested in late summer. Linnaeus considered these seasonal forms as distinct species (*T. hybernum* and *T. aestivum*), but experiments have shown that one kind may be derived from the other in about three years by selecting the most successful of the seedlings that result from sowing either kind in the season normal for the other; that is, by sowing winter wheat in the spring, and spring wheat in the fall.

The official Grain Standards of the United States recognize five classes or grades of wheat, as follows:[2]

Class I, *Hard Red Spring*, with at least 24 distinct varieties, known under at least 80 different names of which the best known is *Marquis*. About one-quarter of the total annual wheat crop of the United States has, for several years, been Hard Red Spring. It is grown chiefly in the Dakotas and Minnesota, and in more

[1] Hackel, Eduard. The true grasses. 1896. Hackel recognized only three divisions as species, namely, *sativum*, *polonicum*, and *monococcum*, the other divisions being called races and sub-races. Other students of the genus have called these sub-divisions species and sub-species. Clark and Martin (U. S. D. A., Bul. 1074. Revised Aug., 1923) suggest that "these ranks would be better designated as subspecies and varieties."

[2] In the discussion of the five standard classes of wheat the papers by J. Allen Clark, John H. Martin and Clyde E. Leighty have been freely drawn upon, particularly U. S. D. A. Farmers' Bulletins Nos. 1280, 1281, 1301, 1303, 1304, 1305, and 1340.

scattered acreage in all the Northern States from Maine to the Pacific coast. It is also extensively grown in Canada, thriving

FIG. 559.—Varieties of Hard Red Spring wheats. *A*, Marquis; *B*, Red Fife. (After J. N. Martin, U. S. Dept. Agr.)

in comparatively cold regions. The varieties of this Class yield valuable flour for bread making. The heads may be bearded or

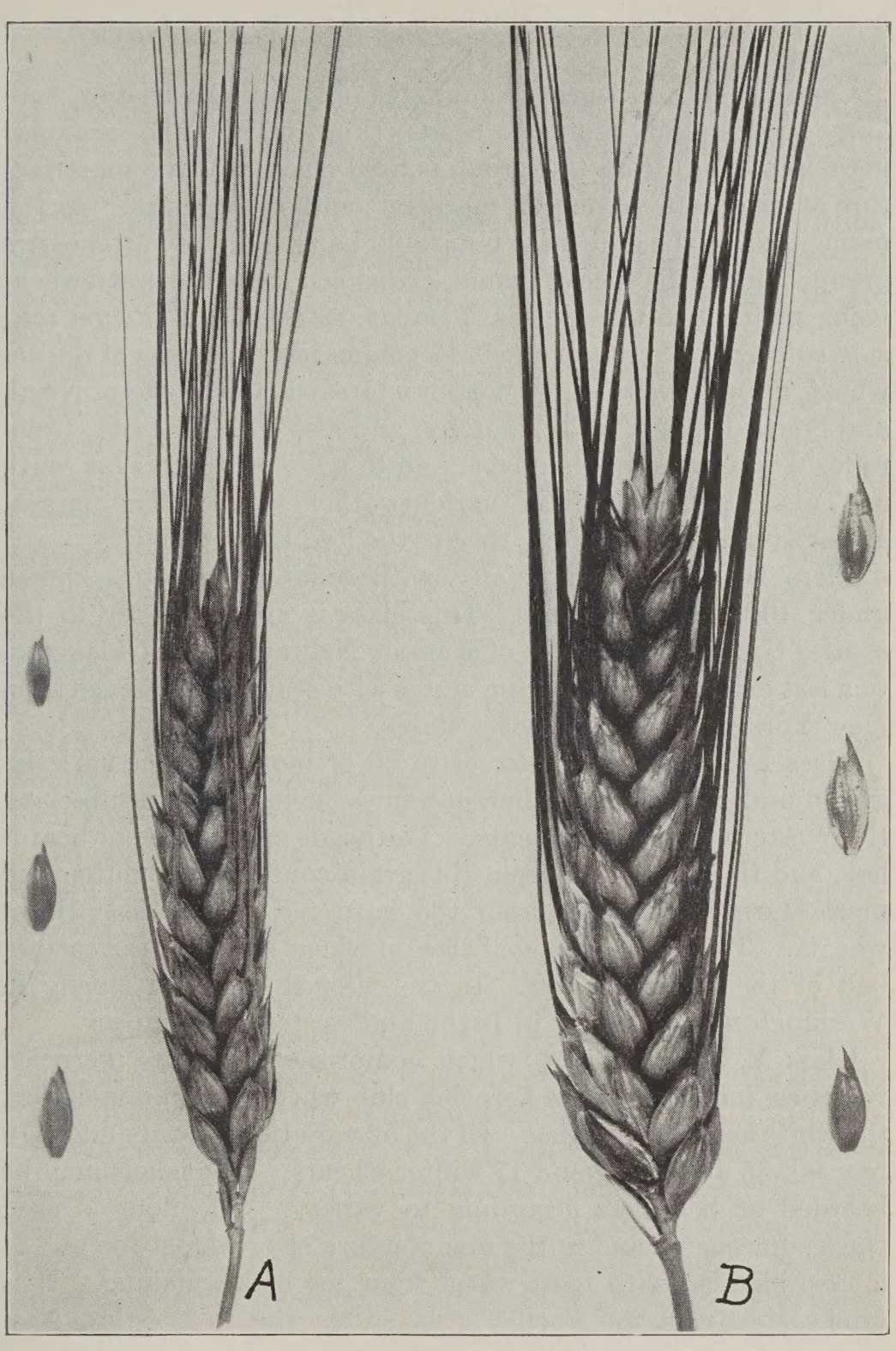


FIG. 560.—Varieties of Durum Wheats. *A*, Pentad; *B*, Peliss. (After Clark and Martin. U. S. Dept. Agr.)

beardless (Fig. 559), and the hard, red grains give the name to the Class.

Class II, Durum wheat, comprising only spring varieties, with long beards and compact heads (Fig. 560). The granular flour (semolina) from this group is used chiefly for the manufacture of spaghetti, vermicelli, macaroni, and other pastes. As the name implies, the grains are unusually hard, and the varieties are grouped under the species' name, *Triticum durum*, the bread wheat being referred to the species, *Triticum vulgare*, or *Triticum sativum vulgare*. There are about 12 commercial varieties of durum wheat, grown chiefly in the northern Great Plains states of North and South Dakota, and Montana, and also in Minnesota, Colorado, Wyoming, and Nebraska, and to a less extent, as far south as Texas and slightly in various other states. The largest acreage is in North Dakota, west of the Red River valley.

Class III, *Hard Red Winter*, with some 12 varieties known under 40 different names. This class is grown chiefly in the central Great Plains states of Kansas, Nebraska, and Oklahoma, to a less extent in neighboring states with scattering acreage from New York to the Pacific coast states.

Class IV, *Soft Red Winter*, with 66 or more distinct varieties grown under nearly 400 different names, including, as a sub-class, the Western Red Club wheats. The heads are bearded or beardless, and the flour made from this grain contains less gluten and more starch than flour from the hard red spring and winter wheats. This is the principal class of wheat grown in the eastern half of the United States. In the west it is grown chiefly in Washington and slightly in Idaho and western Montana.

Class V, *White Wheat*, which comprises the white kerneled varieties, including white kerneled club wheats, but not including the white kerneled durums. Of the 52 varieties (grown under 170 names), 35 are spring and 17 winter wheats. The heads may be bearded or beardless according to variety. The flour is used chiefly for pastry and in the manufacture of breakfast foods. It is also blended with hard wheat flour for bread making. It is grown chiefly in the Pacific coast states and in Western New York, but only scatteringly in other states.

The Club wheats, referred to above, are characterized by small kernels borne in short, thick and very compact heads. In six

sections the heads are beardless, in the seventh bearded. On the basis of these distinguishing characters they are referred to the sub-species, *Triticum sativum compactum.* Their growth is confined chiefly to the states west of the Rocky Mountains.

Polish wheat (*T. polonicum* L.) and Poulard wheat (*T. turgidum* or *T. sativum turgidum*) are bizarre wheats of little or no commercial value in the United States. Poulard has been grown in Europe for nearly 2000 years, but is not an important crop in any country.

Some of the varieties of wheat differ in external characters, others apparently differ only in physiological characters. They differ in yield per acre, lateness or earliness of the crop, resistance to drought, behavior in milling, characteristics of the flour as manifested in baking, resistance to disease (rust), and to extreme cold. In Minnesota, and North and South Dakota the winters are so severe that most winter wheats cannot be successfully grown there, and the crop is composed largely of varieties of the hard red spring and durum wheats. The character of the grain and flour varies more or less with the climate; thus hard red winter wheat, adapted to a cold dry climate, yields soft, starchy grains (resembling soft red winter), when grown in very humid regions.

The solitary, sessile spikelets, of 1–5 flowers each, occur in a terminal spike or "head" of 15–20 or more spikelets. In some varieties the heads are bearded; in others, beardless. The jointed *rachis* or axis of the head is zigzag, as in barley and rye. The flower has three stamens with large anthers on thread-like filaments. As in timothy grass, the first opening of the flowers occurs in the early morning and only about one hour is required for the opening of the flower bud and pollination.

Fertilization of egg-nucleus by sperm-nucleus does not occur until 24–48 hours after pollination, the exact time varying with the variety and with the surrounding conditions of temperature and moisture. After fertilization the embryo begins to form, surrounded by the developing, starchy *endosperm*, outside of which is the nitrogenous *aleurone* layer, and outside of this, in succession, the remains of the nucellus, the inner and outer *integuments* of the seed-coat, and the walls of the ovary, which constitute the *pericarp.* As the grain matures the cells of the ovary wall become

greatly compressed and distorted, and only traces finally remain of the cellular structure (Fig. 561). The parts of the embryo and grain are shown in Fig. 562.

The parts of the wheat-embryo are as follows: The *hypocotyl*, or embryonic stem, bearing at its upper end the *plumule* (first or embryonic bud). At the opposite end of the hypocotyl the first root will develop, and over this end is the embryonic root-sheath or *coleorhiza*. The upper (interior) end of the hypocotyl also bears the *coleoptile*, which surrounds the plumule like a sheath. Attached to the hypocotyl on the side next to the endosperm is

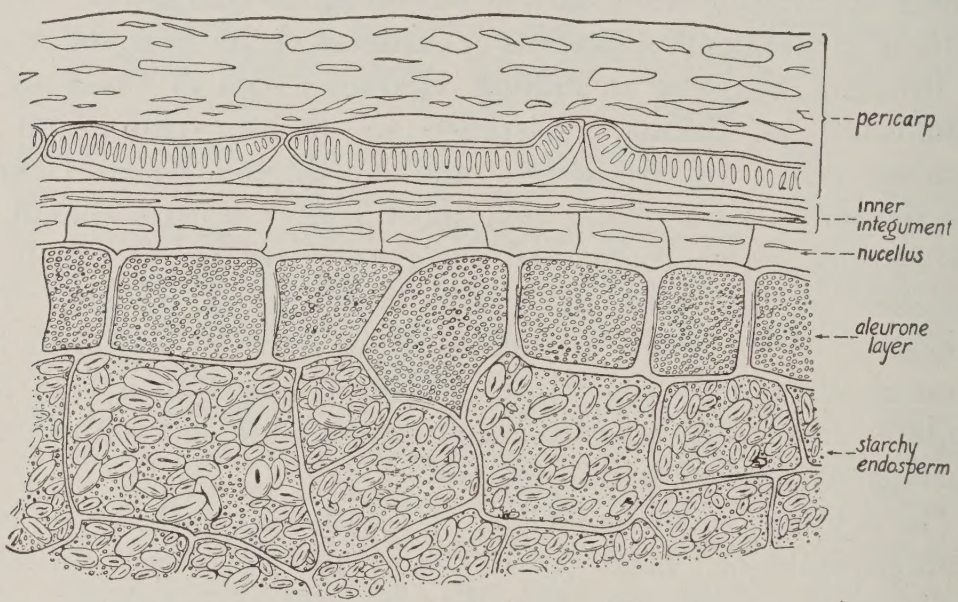


FIG. 561.—Section of a grain of wheat, as seen under the microscope. (After Robbins.)

the shield-like *scutellum*. The outer surface of the scutellum is a *glandular* layer or *epithelium* whose function is, in germination, to secrete an enzyme which acts upon the food stored in the endosperm and digests and absorbs it. At the side of the hypocotyl opposite the attachment of the scutellum is the *epiblast*, which is probably a rudimentary second cotyledon, while the scutellum is the other cotyledon. The outer membrane of the grain, composed of three layers (pericarp, testa, nucellus) forms the "bran," produced in milling.

The common "patent" process flour of which white bread is made is composed chiefly of starch (endosperm), most of the bran and the aleurone layer being removed. "Entire, "or "whole,"

wheat flour contains the inner portion of the bran, with the nitrogenous aleurone layer, while *"Graham"* flour (unbolted wheat meal), contains everything that was in the grain, nothing being removed.[1]

Wheat has been cultivated from prehistoric times; we know that it antedates the Old Testament and the pyramids of Egypt.

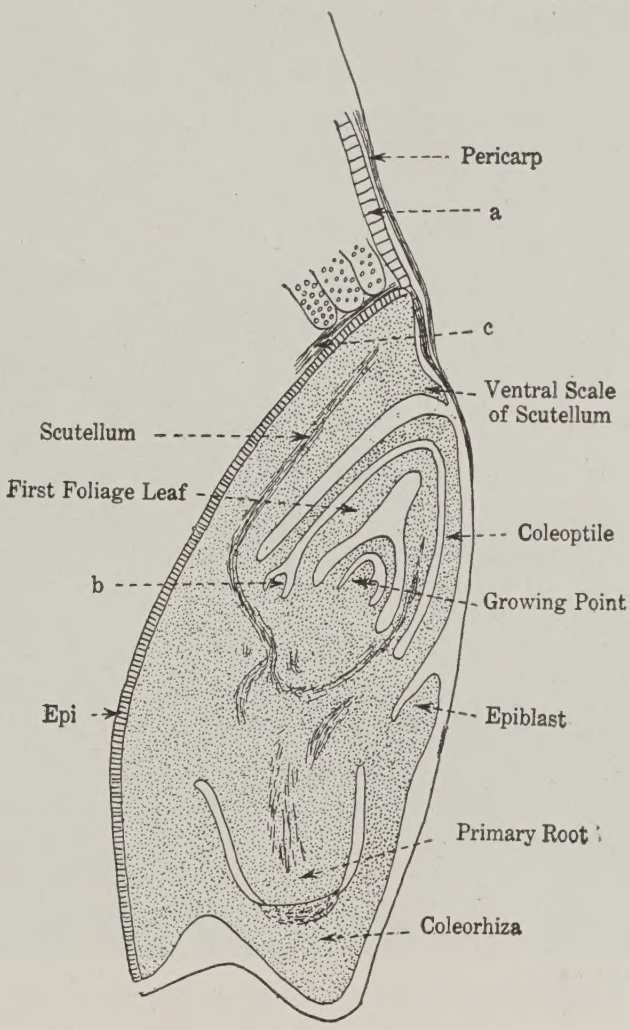


FIG. 562.—Wheat embryo in longitudinal section. *a*, aleurone layer of the endosperm; *b*, bud in the axile of the coleoptile; *c*, crushed empty cells of the endosperm; *epi*, epithelium of the scutellum. (After Percival from Holman and Robbins.)

Ancient traditions attribute the beginning of its cultivation to mythological personages or goddesses, such as the goddess Ceres, or the Egyptian Isis. It is known to have been cultivated in the

[1] Graham flour is named after Sylvester Graham (1794–1851), an American physician who advocated its use. The original Graham bread, following Dr. Graham's recipe, was made without yeast.

late stone age (Neolithic), though the varieties in ancient cultivation were not the same as those of the present, as the plant has been greatly improved by breeding.

About 1909 Aaron Aaronsohn, who made an agricultural and botanical exploration of Palestine under the auspices of the United States Department of Agriculture, discovered in Syria and Upper Galilee, north of Lake Tiberias and on Mount Hermon, the wild *emmer* (*Triticum dicoccum dicoccoides*) which is generally

FIG. 563.—Harvesting and threshing wheat with combined harvester and thresher on a hillside near Moro, Oregon, U. S. A. (Photo by W. A. Raymond through U. S. Dept. Agr.)

regarded as the wild ancestor of some of our cultivated wheats, and as indicating that wheat is indigenous to Syria.

With the possible exception of milk and rice, wheat is probably the most generally used and most important article of human diet. Statistics gathered by the United States Government show that the yearly consumption of wheat in the United States is nearly one barrel (4½ bushels) per person, and that wheat flour and its by-products form about one-fifth of the total food materials of the average American family. Nearly one quarter of the

world's wheat crop is produced by the United States, and the largest annual yield of any one state is in North Dakota, which in 1915 produced, on 8,350,000 acres, nearly 152,000,000 bushels, having a value of more than $132,000,000.[1] A scene in a wheat field in Oregon is shown in Fig. 563.

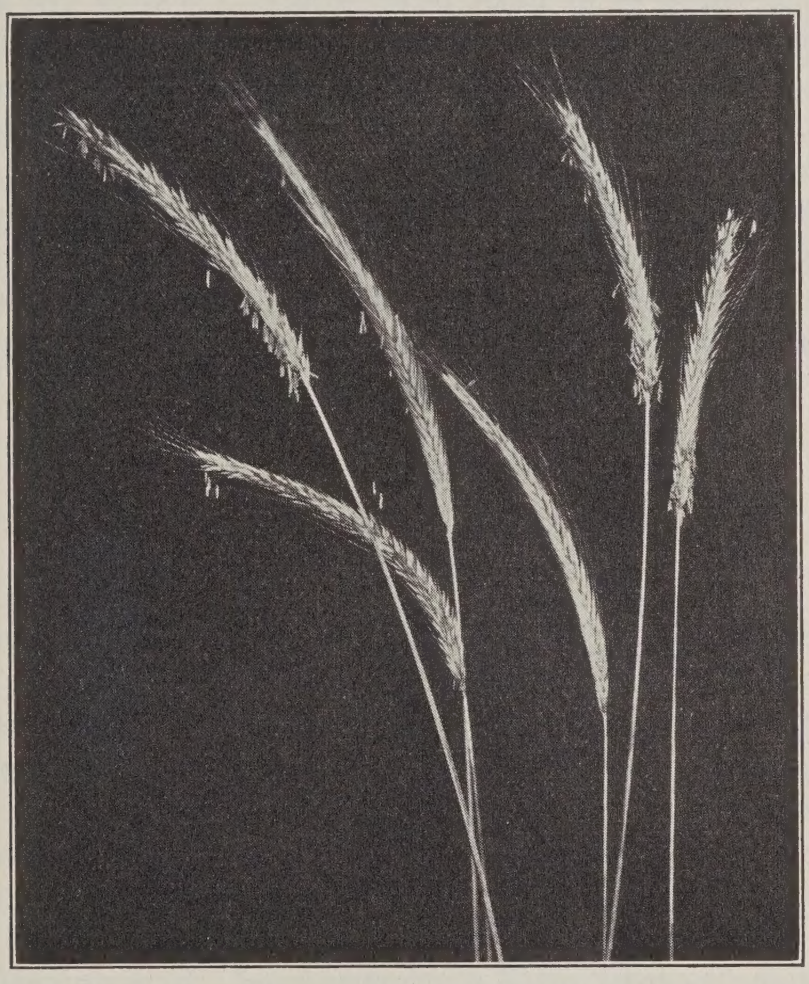


FIG. 564.—Rye (*Secale cereale*). Heads with anthers showing.

RYE

(Barley Tribe, Hordeae)

Rye (Fig. 564), is considered a near relative of wheat, but has not been known so long as a crop plant. It was apparently not

[1] It is interesting to reflect that the name of the greatest wheat producing country in the world, America, is derived from the early explorer, Amerigo Vespucci, and that his name, Amerigo, is in turn derived from emmer, the name of the wild wheat. In more senses than one, therefore, "America" designates "the land of wheat."

known to the ancient Egyptians nor ancient Greeks, and was probably introduced into the Roman Empire not long before the Christian era. It is thought to have come from northeastern Europe, and the wild species (*Secale montanum*) is said to be perennial. The germinating seed has four temporary rootlets instead of three as in most other grains. Winter rye is more common as a crop than spring rye. It is very hardy, being a cold climate plant, in contrast to barley which does best in a warm climate. Rye may be grown as far north as Alaska, and tends to be perennial. It will do well on comparatively poor soil, and is therefore often used for plowing in as a green manure. Rye flour is highly esteemed for bread, the grain and bran are fed to stock, and the germinating grains, like barley, are used in the manufacture of alcoholic beverages. There are only a few varieties.

BARLEY

(Barley Tribe, Hordeae)

Barley (*Hordeum*) has been cultivated from pre-historic times. It was used before wheat for the making of bread, and was, in fact, the principal source of bread flour until as late as the 16th century. Its popularity decreased with the introduction of wheat and potatoes.

Barley differs from wheat and rye in having sessile spikelets of only one flower, and more than one spikelet at the joints of the rachis. The lemma, or flowering glume, is prolonged into a stiff, rough "beard," often 6–8 inches long. In germinating, the plumule becomes twisted. It is used more than any other grain for making malt because it germinates uniformly and rapidly. Varieties with a relatively large percentage of starch (*i.e.*, mealy) are preferred for malting.

There are two distinct species—*Hordeum distichum* with two rows, and *H. vulgare* with six rows of grains on the rachis (Fig. 565). The latter has a variant type—the four-rowed barley. The grain may be sown in spring or fall, and the two-rowed varieties tend to the perennial habit. Aside from its use in malting, barley is used chiefly as food for stock.

OATS

(Oat Tribe, Aveneae)

Oats (*Avena*) came into cultivation at a later date than barley or wheat, and probably in the temperate regions of eastern Europe. They have been cultivated in Europe from prehistoric

FIG. 565.—Types of Barley (*Hordeum*). *a*, six-rowed bearded (Wisconsin Winter); *b*, two-rowed bearded (Omar); *c*, six-rowed hooded (Reid's Triumph); *d*, six-rowed beardless (*Mortoni Nigritonsum*).

times, but appear to have been unknown to the ancient Hebrews, Egyptians, and Chinese, and to the Greeks and Romans of classic times. They are much used as feed for horses and stock, but also widely used as human food—particularly in Scotland and Ireland.

In all the Aveneae tribe the inflorescence is in panicles (Fig. 566). Oats have more leaves than wheat, the leaf-blade is broader as a rule, and the ligule better developed. The panicle may reach a length of twelve inches, and may have as many as 75 spikelets, each borne on a flexible stalk or pedicle, and usually containing two mature flowers and a sterile third flower (Fig. 566). The ripened grain is enclosed by the flowering glume and palea, which, together, are called the "hull." This is quite

FIG. 566.—Oats. *A*, upper part of panicle; *B*, spikelet in flower; *C*, glume; *D*, lemma with awn; *G*, scales (lodicules) at the base of the ovary; *J*, styles bearing the feathery stigmas. (After Nees von Essenbeck, from F. L. Sargent.)

different from the bran of wheat or the hull of Indian corn, which are composed of the three outer layers of tissue of the grain —pericarp, testa, and nucellus. As in wheat, the surface of the pericarp is hairy. There are both spring and winter varieties, some of which are more resistant to Rust than are others. They are all self-fertilized except when artificially crossed. Their water requirement (*Cf.* p. 31) is greater than that of corn, but slightly less than that of barley.

TIMOTHY

(Timothy Tribe, Agrostideae)

One of the most important forage crops is Timothy grass (*Phleum pratense*), of the Timothy Tribe (Agrostideae). The flat, one-flowered spikelets form a cylindrical, spike-like panicle, somewhat resembling a tiny cat-tail (Fig. 567). In fact, in England the name *Cat-tail grass* (or *Catstail*) is given to all species of Phleum.[1] The 8–20 culms, arising from a perennial base, attain a height of 1.5–2 feet. There are 3–8 flat leaves on each stem. The plant is cultivated in meadows for hay and is, perhaps, the most important plant grown for that purpose. The flower buds open and the anthers shed their pollen all in the space of about one hour and a half. Self-pollination is the usual method, but cross-pollination is possible and often occurs in nature. The first opening of the flower-buds (*anthesis*) occurs in the very early morning, before sunrise, the upper third of the inflorescence coming into bloom first; blooming lasts about 7–10 days.

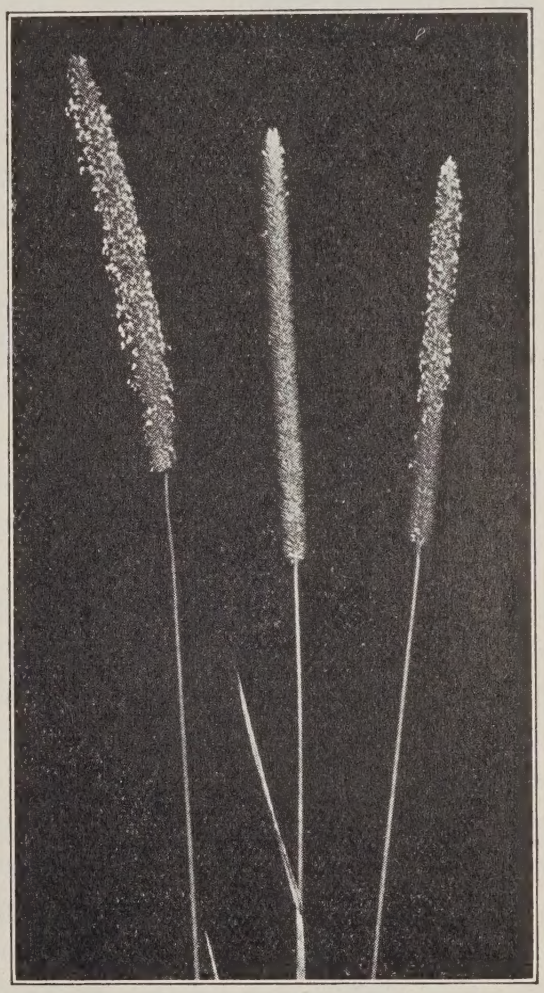


FIG. 567.—Inflorescence of Timothy grass (*Phleum pratense*). (Photo by E. M. Kittredge.)

The best time to cut timothy for hay is just at the close of blooming when the yield of dry matter is greatest. If the plant

[1] The Latin name (from the Greek, *phleos*, φλέως) was applied by the Roman writer, Pliny, to a kind of reed. Timothy is a European grass introduced into Maryland about 1720 by Timothy Hanson, whence the name, timothy.

is not cut then the food elaborated in the leaves and other green parts passes, some to the ripening ovaries ("seeds"), and some down to the corms or bulbils forming at the axils of the lower leaves—from six or eight to as many as 20 in number. These corms produce new shoots the following spring.

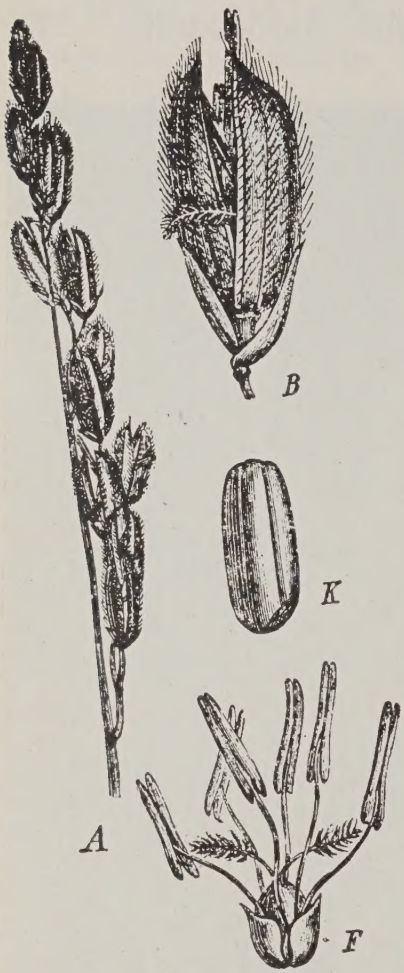


FIG. 568.—Rice (*Oryza sativa*). *A*, part of inflorescence of beardless rice, natural size; *B*, spikelet; *F*, a flower with its two scales or lodicules. *K*, ripe kernel. *B*, *F*, and *K*, enlarged. (After Nees von Essenbeck, from F. L. Sargent.)

RICE

(Rice Tribe, Oryzeae)

Rice (*Oryza sativa*) is economically the most important of the tribe Oryzeae and is, in fact, one of the most important of all food plants, being the chief article of diet for about one-half the human beings of the world. In China, and elsewhere in Asia, it forms about one-half the food of the people. It is used extensively in the manufacture of starch, but is not much used in the United States for pastry or bread, because of its low protein content. This lack of protein in rice is compensated for in China by using with it the soy bean (*Glycine Soja*), which is rich in protein and fat.

There are numerous varieties of cultivated rice, including the lowland and upland types. More than a dozen varieties are grown in the Southern States of the United States, and also in Honduras and Japan; they are distinguished by the size and color of the grain, number of tillers per plant, and otherwise.[1] Like other small cereals, rice tillers freely—that is, it produces many culms per seed. The one-flowered spikelets on short pedicels form a compact panicle, somewhat rough toward the

[1] Cf. Chambliss and Jenkins. Some new varieties of rice. U. S. D. A. Dept. Bull. 1127. Jan. 12, 1923.

tip, otherwise smooth (Fig. 568). Underneath the two outer small glumes are two others, rudimentary. The flowering glume (*palea*) is often tipped with an awn, and the *six stamens* distinguish the rice flower from that of all other cereals. The comparatively long ovary bears two styles, united below, and each terminated by a feathery stigma. The fruit is a *caryopsis* to which the flowering glume and palea adhere after threshing. Rice in this stage (in the husk) is known as "paddy" rice, or "rough rice."

The lemma and palea form the so-called "hulls," while the "cuticle" is composed of the pericarp, seed-coat (*testa*), and nucellus, all corresponding to the "bran" of wheat. Rice matures in about 120–150 days after planting.

The hulls and embryo are removed in milling. The rice is then polished by being rubbed against pieces of sheepskin, tanned so as to be specially soft. In polishing, the cuticle is removed and therewith most of the nitrogenous (proteinaceous) tissue, thereby improving the looks of the grain, but greatly reducing its food-value. Hence, unpolished or brown rice is superior to polished or white rice from a dietary standpoint.

The great importance of rice—especially among Orientals—is evidenced by the fact that, in the ancient annual Chinese ceremony of sowing five kinds of seeds, four of them might be sown by princes of the imperial family, but the rice seed was sown by the Emperor himself. This ceremony was instituted 2800 years B.C. Rice was probably first cultivated in China where the great expanses of alluvial plots and deltas afford an almost ideal soil condition. It was undoubtedly growing wild in India before its cultivation was introduced there from China. From India its cultivation extended gradually westward through Babylonia and Syria into Egypt. From Egypt it was introduced by the Saracens into Spain, where it is still called by the Arab name *arroz*. In 1694 the captain of a merchant ship from Madagascar presented a bag of rice to the Governor of South Carolina, and the crop raised from these seed in Charleston, S. C., marks the beginning of rice culture in America. The principal rice areas of the United States are given as follows by Hunt:[1]

[1] Hunt, Thomas F. The cereals in America, New York, 1920. pp. 357–381.

1. The delta land and inland marshes of the south Atlantic States.
2. The alluvial lands along the Mississippi River.
3. The prairie soil of southwestern Louisiana and southeastern Texas.

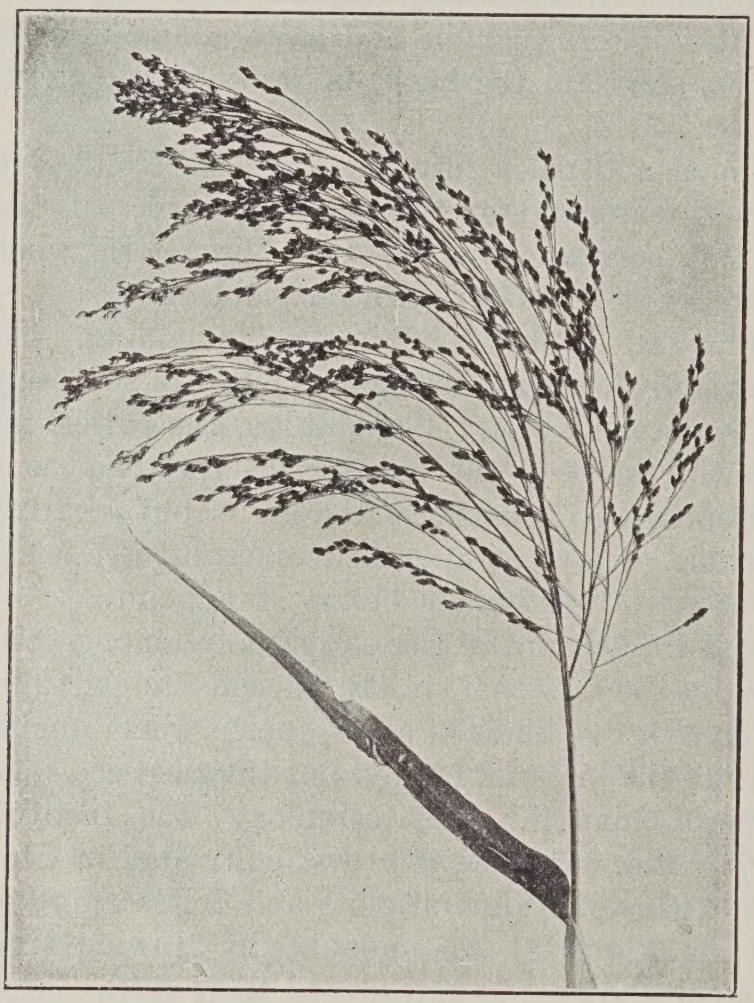


Fig. 569.—Inflorescence of Broom-corn Millet (*Panicum miliaceum*). (After Robbins.)

Approximately one half the crop of the United States is raised in Louisiana, and somewhat less than 20% in South Carolina. Rice is now also extensively grown in the upland prairie region of east central Arkansas (under irrigation from wells), in Texas and, since about 1912, in California.

The wild rices, *Zizania aquatica* (New Brunswick to Manitoba and south of Florida and Texas) and *Zizania miliacea* (a southern

species, common in Louisiana), also belong to the tribe Oryzeae, and the grain of the former was used as food by the North American Indians, by whom it was cultivated to a slight extent. The southern species is of value only for hay. The Chinese wild rice, *Z. latifolia*, is cultivated in standing water and the young shoots become swollen by the growth of a parasitic fungus, which acts in a manner similar to corn smut. These swollen shoots are considered a delicacy and are called "Water-bamboo," though not related to the bamboo (except, of course, that both are in the family Gramineae).

MILLET

(Millet Tribe, Paniceae)

The name millet has been applied to several species in various genera, among which the following may be mentioned here. Broom-corn millet (*Panicum miliaceum*), is the common millet of Europe and cultivated there and in America as a cereal and hay crop (Fig. 569). This is the plant referred to by the Romans as *milium*, whence our name. It is also called Proso Millet and Hog Millet. Barnyard Millet is *Echinochola crus-galli*. Another species, Japanese barnyard millet (*E. frumentosa*), is grown in Japan and India for forage and to a less extent as human food

The Foxtail millet, *Setaria italica*, is an annual grass having numerous varieties in cultivation. It is believed to be native in southern Asia, and has been cultivated in China from as early as 2700 years before Christ. Seeds of it have been found in the remains of the Lake Dwellers of the Stone Age.

CHAPTER XXXVII

MONOCOTYLEDONS (CONTINUED)

THE SORGHUMS

(Sorghum Tribe, Andropogoneae)

The genus *Holcus* L. (= *Sorgum* Persoon), of large economic importance, comprises about 13 species of wide distribution in

FIG. 570.—*Holcus halepensis*. Johnson Grass. (After Britton and Brown.)

the tropics and warm temperate regions. Johnson grass (*Holcus halepensis*),[1] introduced into America from southern Europe and Asia, is thought by some to be the wild original of the cultivated sorghums (Fig. 570). It is widely distributed in the United States east of the Mississippi River. The genus comprises annual and perennial grasses, with long, comparatively wide leaves, and

[1] Synonyms, *Andropogon halepensis* Brotero; *Sorghum halepense* Persoon.

the flowers in a large terminal, spike-like, panicle, called a "head." The spikelets usually occur in pairs or, toward the top, in threes. In the paired spikelets one is sessil and fertile, the other stalked and staminate. The two glumes of the fertile spikelet inclose one perfect flower and, below it, a sterile or staminate one. As commonly in grasses the anthers are very large in comparison with the filaments The sessile ovary

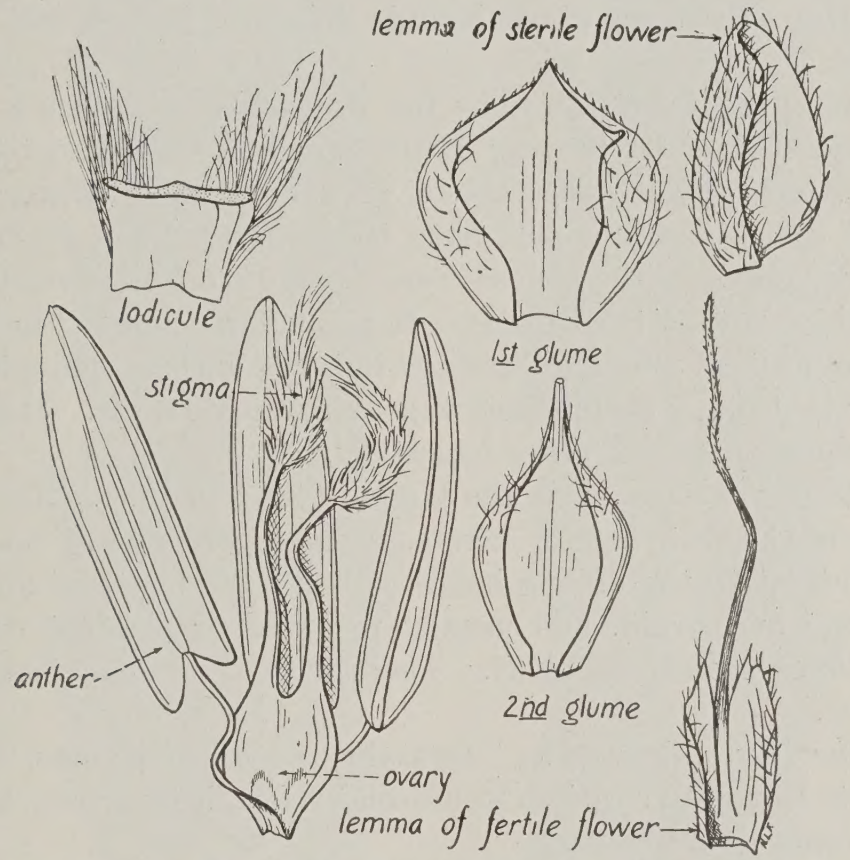


FIG. 571.—Spikelet of Sudan Grass (*Holcus Sorghum Sudanensis*), one of the hay sorghums. Lodicule × 10; other figures × 5. (After Robbins.)

(*smooth at the tip*, in contrast to oats, barley, wheat, and rye) bears two styles tipped with "bushy" stigmas (Fig. 571).

Since Sorghums have a root system about twice as large as that of corn, but only about half as much leaf surface, they can withstand, better than corn, a climate where the evaporating power of the air is excessive.

The cultivated varieties of sorghum (*Holcus Sorghum* L.) fall into four groups, as follows:[1]

[1] Following Ball and Rothgeb. Grain-sorghum experiments in the panhandle of Texas. U. S. Dept. Agr. Bul. 698. Washington, 1918.

1. *Grain sorghums,* which include such well-known groups as *Kafir, durra* and *milo,* and *Kaoliang,* and also less commonly grown groups, such as *shallu,* and others.

2. *Sorgo,* or forage sorghum, known also as sweet or saccharine sorghum, and improperly called "cane" or "sugar cane."

3. *Broom corn,* which includes two rather distinct varieties, Standard and Dwarf.

4. *Hay sorghums,* which include Johnson, Sudan, and Tunis grasses.

Among the grain sorghums the Kafir (Fig. 572) has a stout, short-jointed stalk, bearing 12–16 broad leaves, close together below, but farther apart above. Kafir was first cultivated in South Africa and is named from the native tribe of Kafirs. It has been grown in the United States since 1876, and is much more drought-resistant than maize. It is similar to maize, however, in composition and digestibility, but has such a characteristic flavor that many people have to acquire a taste for it. It is used in making bread and other bakestuffs.

Milo was first grown in the United States in 1882. The stalk bears 9–11 short, narrow leaves, and contains almost no juice. In contrast to the oblong heads of kafir, the heads of milo are compact and ovoid, and usually recurved or pendent, though sometimes erect (Fig 573). There is a Dwarf and Standard variety.

White Durra (known as "Jerusalem corn" in Kansas, and as "White Egyptian corn" in California) is now little grown, having been replaced by Kafir.

The *Kaoliangs,* with pithy stalks and short, narrow leaves, have low fodder value and low yield of grain. The name is a Chinese word, pronounced *Kŏw-lĕ-ang,* and meaning "tall millet." Although not grown extensively in the United States they are an important crop in the eastern half of China, and in Manchuria, where the seeds are used as food for man and beast, and in making an alcoholic drink. The stalks are used for fuel, and the stems and leaves for thatching, fences, and in the manufacture of baskets, mats, brooms, and other articles. In some countries the grain sorghums are the chief article of diet.

The *saccharine sorghums* (Sorgo) are cultivated for their sweet juice from which syrup and sugar are made. There are numerous

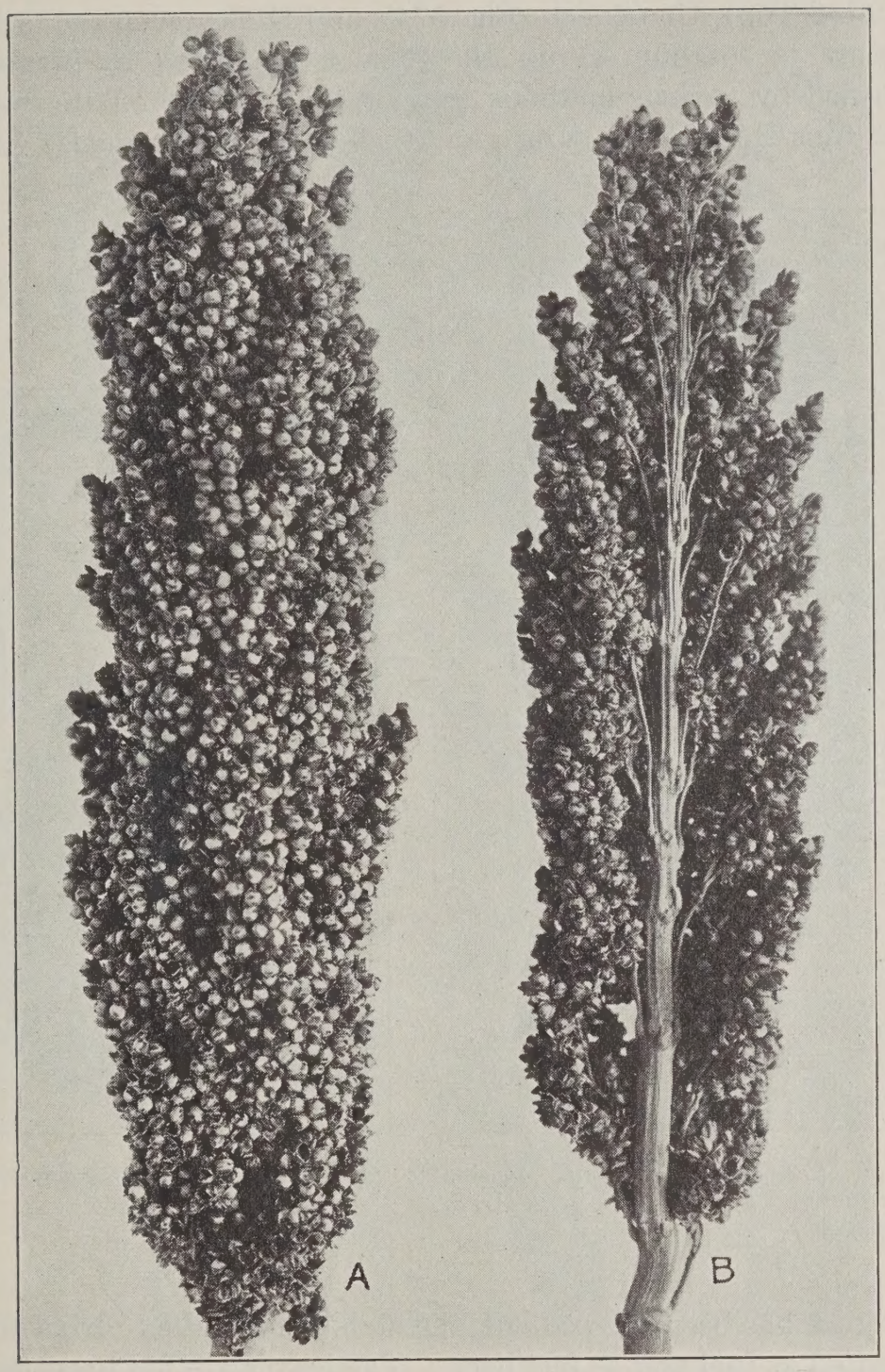


FIG. 572.—*A*, Head of Kafir sorghum; *B*, showing inside construction of same. (U. S. Dept. Agr.)

varieties, the more important of which are Amber, Orange, Sumac (or Red Top), Gooseneck (Fig. 574), and Honey. In the manufacture of sorghum syrup, the juice is extracted by pressure, clarified by various methods, evaporated to drive off the water and thus thicken the syrup, and then bottled or canned. After

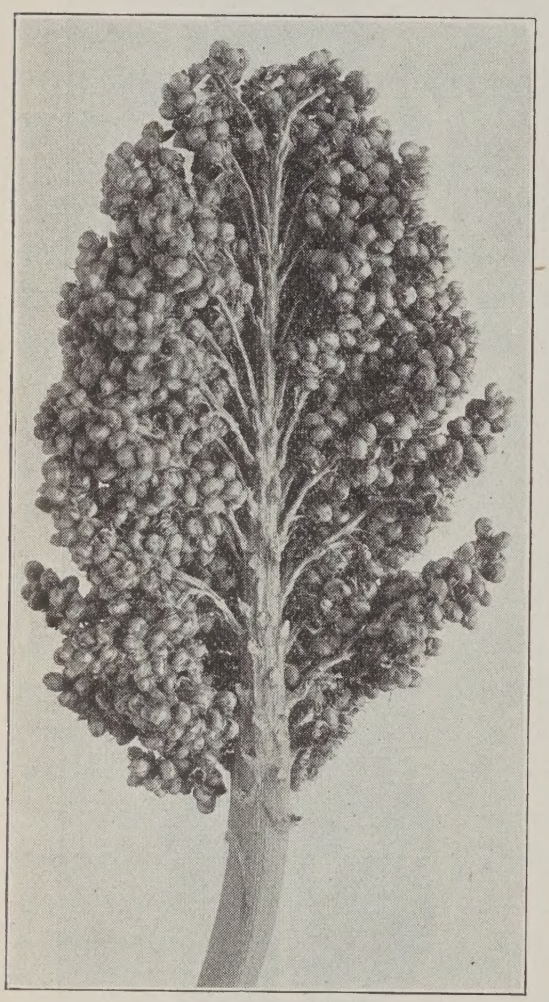


FIG. 573.—Milo sorghum. Inside construction of a typical head. (U. S. Dept. Agr.)

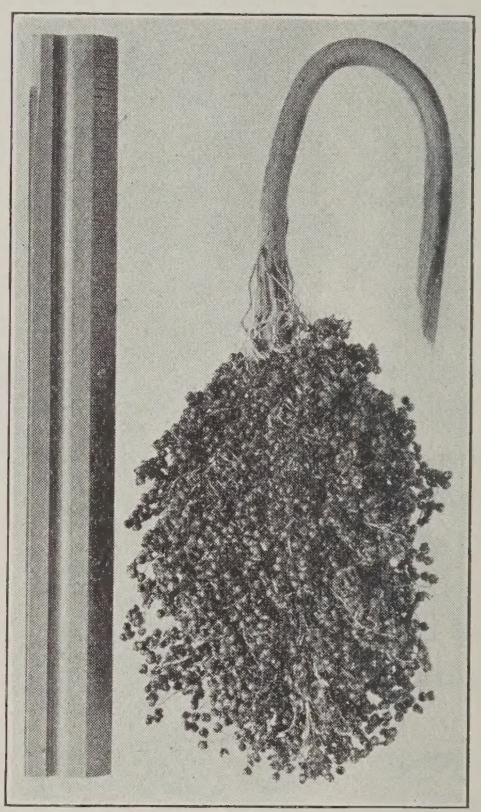


FIG. 574.—Head of Gooseneck Sorgo. (U. S. Dept. Agr.)

the juice has been pressed out, the stalks (now called "bagasse") are used as fuel and as fertilizer. The leaves are fed to cattle or plowed under as fertilizer.

Broom corn, from the branched inflorescence of which all kinds of brooms are made, is a special kind of sorghum. The inflorescences or heads are known to the growers as "brush" (Fig. 575).

FIG. 575.—Broom corn. Different types of heads. *A*, good type, round fiber; *B*, coarse flat fiber; *C*, crooked head; *D*, short fiber and large central stem. (U. S. Dept. Agr.)

There are three well recognized varieties of broom corn, as follows:

1. *Standard,* which reaches a height of 8–15 feet, depending upon the conditions of climate and soil. There are 9–11 leaves, and the heads, 18–24 inches or more in length, grow out of the upper leaf-sheath or "boot." They are so firmly attached to the upper node that they cannot be broken off, and must be harvested by cutting.

2. *Dwarf* broom corn is only 3.5–6 feet high, its low height being due to the shortness of its internodes. It has 10–13 leaves, and heads 15–22 inches or more long. In contrast to the Standard variety, the heads remain more than one half enclosed in the upper leaf-sheath. In harvesting they may be jerked or pulled off.

3. *Acme* (Dwarf Standard) was developed as a sport from Standard. Although of similar height to Dwarf, its "brush" is about the same length as that of Standard, which makes it more valuable than Standard as a broom corn (Fig. 576).

The principal hay sorghum is *Sudan grass,* related, as stated above, to Johnson grass. Its botanical name (following Hitchcock[1]) is *Holcus Sorghum Sudanensis.* This sorghum was introduced from Africa under the name *Andropogon halepensis,* but Piper separates Johnson grass from Sudan grass on the basis of presence or absence of a rhizome—present in Johnson grass, absent in Sudan grass. As separated on the basis of this character the natural ranges of these two species do not overlap, Sudan grass being confined to that part of Africa south of the equator, and Johnson grass being confined to southern Europe, Asia Minor, and the northern border of Africa.

The first Sudan grass seed was received in the United States in March, 1909, as a gift to the Department of Agriculture from the Director of Agriculture and Lands, Sudan Government, Khartum, Sudan, whence the name. It proved immediately successful in the United States. In contrast to Johnson grass, which is a perennial, Sudan grass is an annual. Its slender stems grow to a height of 4–6 feet, bearing numerous soft leaves, flowers in a loose

[1] *Holcus Sorghum Sudanensis* (Piper) Hitchcock. (U. S. Dept. Agr. Bul. 772) = *Andropogon Sorghum Sudanensis* Piper.

open panicle, numerous tillers, and only occasionally branches.[1] The absence of rhizomes makes it impossible for Sudan grass to become a troublesome weed like Johnson grass. Although Sudan grass requires more water to produce a pound of dry matter than does corn, millet, or other sorghums, it is very drought-resistant, and therefore gives a good crop in regions of comparatively low rainfall.

FIG. 576.—Plants of Acme (Dwarf Standard) Broom corn. (U. S. Dept. Agr.)

SUGAR CANE

(Sorghum Tribe, Andropogoneae)

Sugar cane (*Saccharum officinarum*), is a tropical, perennial grass which attains a height of 8–15 feet or more. It is grown chiefly in Louisiana as a source of "cane sugar" (Fig. 577). In states adjacent to Louisiana it is grown also as a forage plant.

[1] Cf. Vinal and Getty. Sudan grass and related plants. U. S. Dept. Agr. Bul. 981, Washington, D. C., 1921.

The inflorescence is a panicled raceme (Fig. 578). One of the paired spikelets is sessile, the other stalked (pedicillate.) The solid, jointed stems yield a copious juice which is the source of the sugar. There are about ten species in the genus.

FIG. 577.—Planting sugar cane (short lengths of the stem) in a field in Hawaii. (Photo by Miss Frances Marshall.)

CORN

(Corn Tribe, Tripsaceae)

It is difficult to realize that corn, which means so much in modern life, was wholly unknown to the ancient world of the eastern hemisphere. In fact the word corn which, in America, refers to "Indian corn" or maize (*Zea Mays*), is used in England as a generic name for grain, especially wheat. The plant is a native of America, and was not introduced into Europe until after the voyage of Columbus. There is no word for this plant in the Greek or the Sanskrit languages. The generic name *Zea*

(Greek, *zeia*) was first applied to spelt, a species of *Triticum*. The name *Mays* is American (Haytian Indian, "Mahiz"), and was first used by the herbalist, Dodoens, in 1563.[1] (Fig. 579). How strange for us to think of thousands of years of European agriculture without any knowledge of Indian corn!

FIG. 578.—Sugar cane (*Saccharum officinarum*). (After Hitchcock. U. S. D. A. Bull. 772.)

FIG. 579.—*Zea Mays*. One of the earliest published illustrations reproduced from the *Cruydt-Boeck*, of Dodoens (1644), where it is called Turckisch-Korn.

Maize was found widely cultivated in North America at the time of its discovery by the Spaniards, ranging from the Argentine to the Great Lakes and from the Altantic to the Pacific oceans. Columbus found it growing in Hayti, the Piligrims found it in 1620 at Plymouth, and Cartier found Hochelaga (now Montreal)

[1] With reference to *Zea Mays*, Dodoens says: The Netherlanders call this plant *Torchs-Koren*—in Latin *Frumentum Turcicum;* the Germans, *Turckisch Korn;* the French, *Blé de Turquie;* the natives of America (the adjacent islands) call it *Maiz*. *Cruydt-Boeck*. Ed. of 1644, p. 822.

in 1535 surrounded by large cornfields. The planting of corn and of other crop plants had a tendency to make the roving Indians remain longer in one place, for it was necessary to cultivate the

FIG. 580.—Teosinte (*Euchlaena mexicana*). 1, plant showing habit (about one-twelfth natural size); 2, a branch showing the staminate panicles at the tip and the pistillate or fertile ears in the axils of each upper leaf; 3, an ear (slightly enlarged); 4, four grains, each with its long feathery stigma (enlarged); 5 and 6, different views of the mature grain. (After Piper. U. S. Dept. Agr. Farmers Bull. No. 1433.)

plant, and to wait until it matured. The growing of corn, therefore, has been an important factor in the civilizing of man. *Zea Mays* has never been found growing wild, but it is supposed,

from certain evidence, that its native home was the plateau region of Mexico or of northern South America. Columbus reported passing through 18 miles of corn fields. The various horticultural varieties—sweet, dent, flint, and pop, were all known to the Indians and cultivated by them. The first sweet corn, in fact, is said to have been obtained by the white man from the Susquehanna Indians, in 1779, and cultivated near Plymouth, Massachusetts.

The Tribe *Tripsaceae* also includes Gama grass (*Tripsacum dactyloides*), a common wild plant, especially of the prairie regions

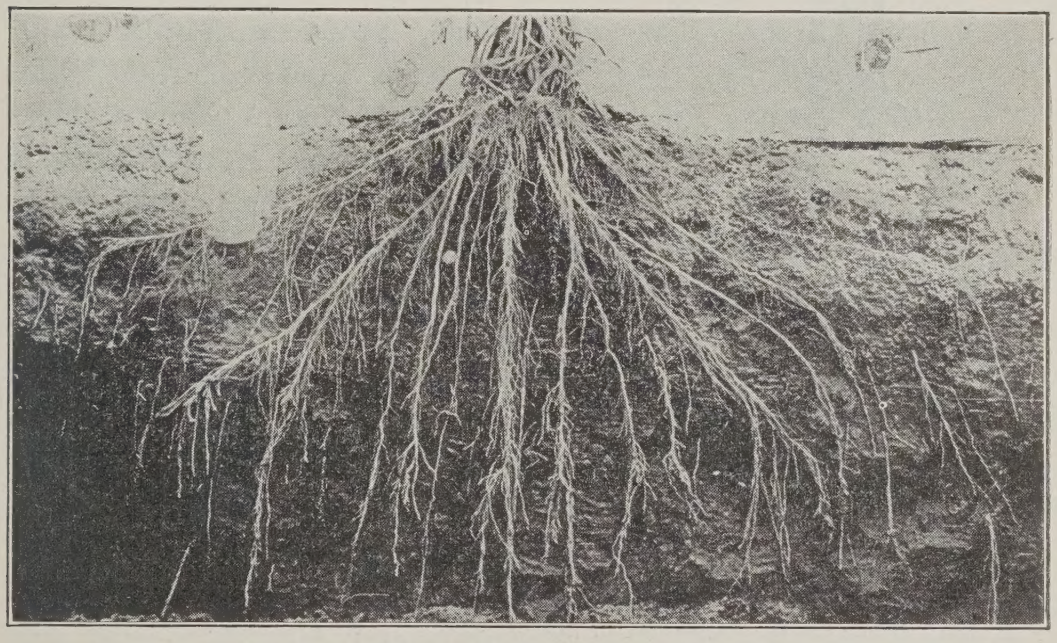


FIG. 581.—*Zea Mays*. Root-distribution at silking time. (After Hartley. U. S. Dept. Agr. Yr. Book. 1903.)

of the southern and central United States, and north to Connecticut; and Teosinte (*Euchlaena mexicana*), cultivated in some of the warmer regions of the United States for fodder (Fig. 580).

The ancestry of maize, the country where it is indigenous, and its relation to other grass plants are not definitely known. It has never been found except under cultivation. One theory is that it originated as a hybrid between certain wild plants; another that it is descended from the wild species, *Zea canina*. Studies of Weatherwax[1] lead him to the opinion that *Zea Mays*,

[1] Weatherwax, Paul. The evolution of maize. Bul. Torrey Bot. Club **45**: 309–342. Aug., 1918.

Teosinte, and *Tripsacum* "have descended independently from a common ancestral form now extinct."

The *root system* of *Zea Mays* is fibrous, and occupies the soil to a depth of 3 feet, on the average, in some cases reaching down 4 or 5 feet (Fig. 581). There are three general kinds of roots: 1. Prop roots; 2. main vertical roots; 3. main lateral roots. Prop roots develop in whorls at various levels *above the surface of the soil* (Fig. 582). On reaching the soil they begin to branch and the rootlets act as organs of absorption as well as holdfasts. As stated on page 31, Indian corn is a plant of low water-requirement as compared to wheat, potatoes, alfalfa, and numerous other crop-plants. The root system also requires good aeration. Every farmer is familiar with the poor stand in a poorly drained area of any cornfield (Fig. 583).

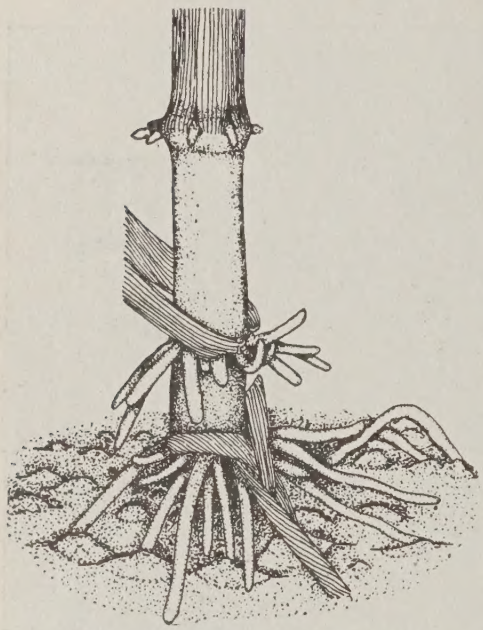


FIG. 582.—Prop roots of Indian Corn. (After Weatherwax.)

The *stem*, as in most "grasses" is jointed, with solid *nodes* and *internodes* filled with fibrous pith (Fig. 584). The fibers are fibro-vascular bundles. The stem is not cylindrical (as seen in cross-section), but has a well defined groove on the side next the leaf. Except in raising fodder corn, the numerous secondary branches or "suckers" are undesirable, for their roots take a great deal of moisture and food materials from the soil, although the suckers themselves seldom, if ever, bear ears. By careful selection in breeding the suckers may be eliminated (Fig. 585).

There are from 8–20 *leaves* borne alternately on the stem. Each leaf has three distinct parts or regions: *base, blade, ligule* (Fig. 586). The leaf-base clasps the stem tightly, and at the base of the blade is the ligule which presses closely up against the stalk. Corn sheds rain water centripetally, the water running down the upper surface of the blade as down a channel or trough. It is prevented from lodging between the stem and the

leaf by the closely-fitting ligule, and the numerous plant-hairs on the ligule and leaf-base. (Fig. 586.)

Zea Mays is *monoecious*.—The staminate inflorescence, or *tassel*, is composed of a central axis or spike bearing several lateral branches which, in turn, may be either branched or simple. The spikelets normally occur in pairs, one stalked and the other sessile (Fig. 587, at 3 and 5). Exceptional cases have been

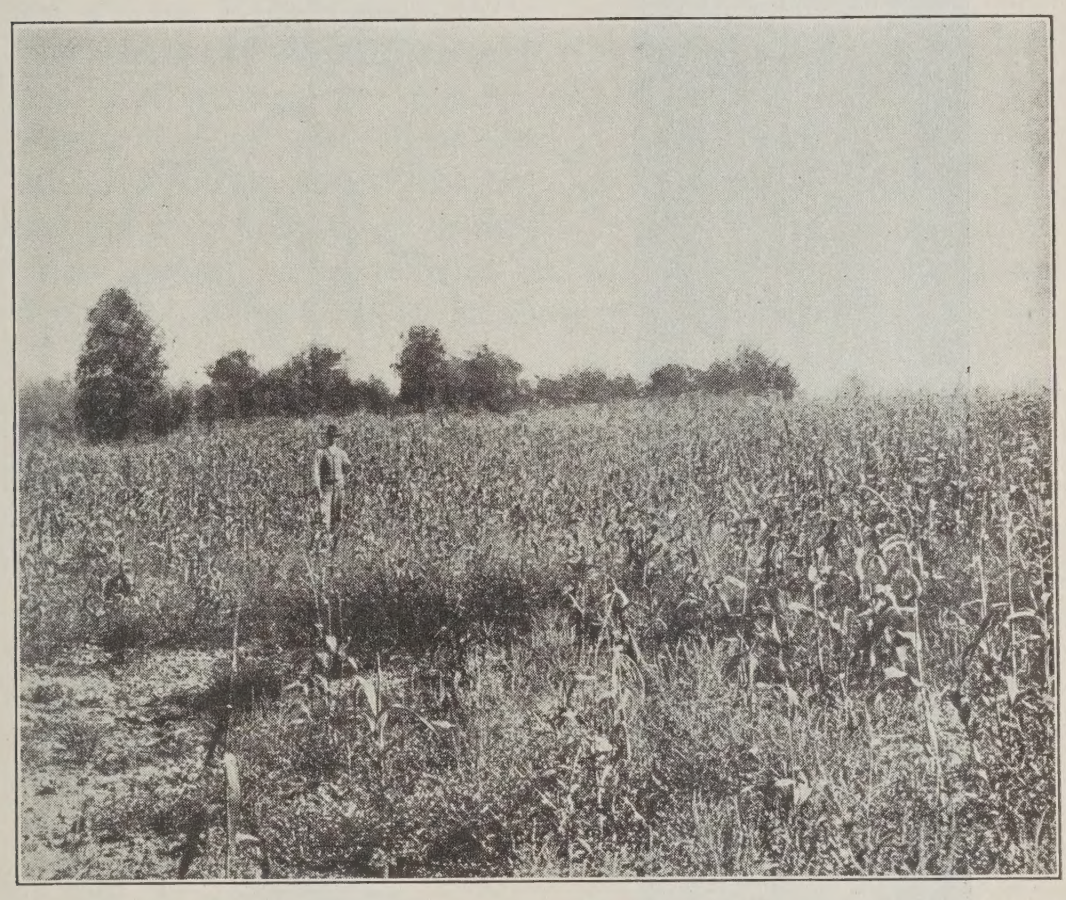


Fig. 583.—Field of Indian Corn, showing poor yield on a poorly drained portion of a field. (After Hartley. U. S. Dept. Agr. Year Book. 1903.)

recorded[1] of one, three, or even more flowered spikelets (Fig. 587, at 4).

The structure of the *staminate spikelet* is shown in cross-section in figure 588. Up to maturity two empty *glumes* enclose the remainder of the spikelet, the lower overlapping the edges of the

[1] In connection with the description of the flowers of maize I have either paraphrased or drawn freely on Weatherwax (Bull. Torrey Club **43**: 127–144. March, 1916) *Ibid.* **45**: 309–342. Aug., 1918), and the papers cited by him. Quotes are omitted for convenience.

latter. The two flowers have the same structure, but the upper one matures before the lower. Each staminate flower possesses the rudiment of a pistil. Within the glume is the lemma (flowering glume), next within this the fleshy *lodicules*, then the stamens,

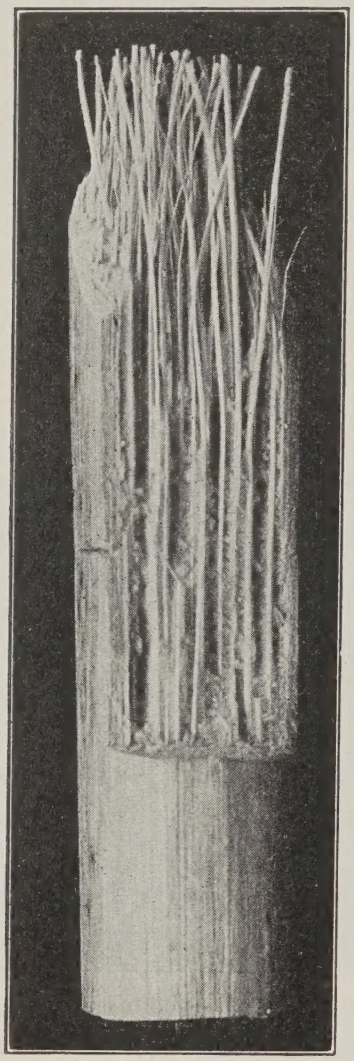


Fig. 584.

Fig. 585.

Fig. 584.—Fibro-vascular bundles in a corn stalk (*Zea Mays*).

Fig. 585.—*Zea Mays*. Highly specialized plant with the suckers bred out. All the energy of the plant goes to the development of a single ear. (After Weatherwax.)

arranged at the angles of a triangle, and then the *palea*. Within the triangular area formed by the stamens Weatherwax found, in every staminate flower he examined, the functionless rudiment of a *pistil*.

The *pistillate spikelet* (Fig. 589) is also two-flowered, and each flower resembles the staminate flowers in structure except that different organs are aborted or developed, as the case may be. The thick, empty glumes do not completely enclose the other parts (except in pod corn, where the glumes form the "pods"). The lemma and palea are shorter and thicker than the glumes, ceasing development about the time of fertilization, and forming the red or white, more or less chaffy covering that remains on the cob after the grains are removed. When fertilization does not take place the *flower bracts*

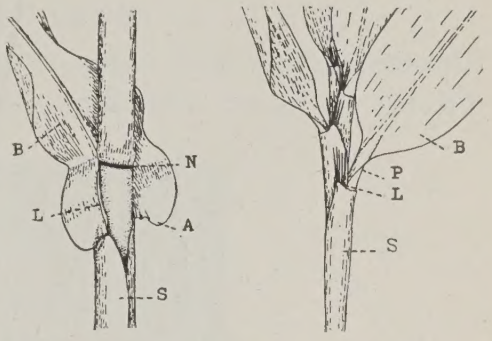


FIG. 586.—Parts of the leaf of *Zea Mays*. (After Weatherwax.)

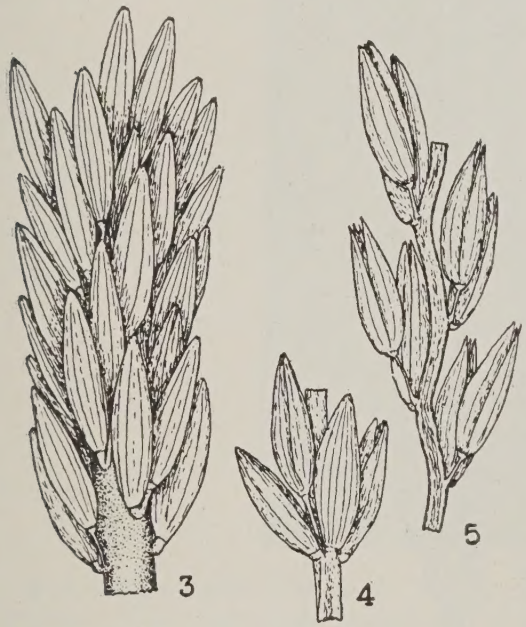


FIG. 587.

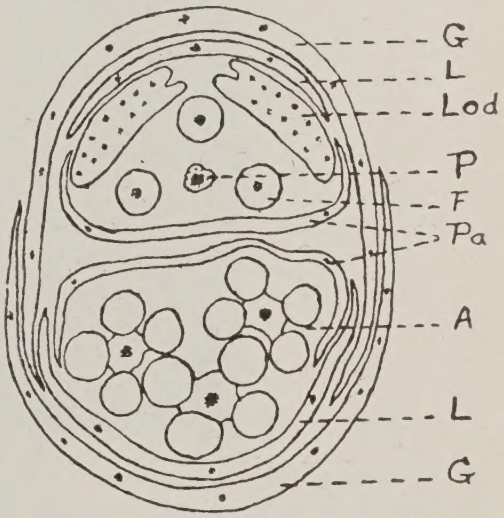


FIG. 588.

FIG. 587.—*Zea Mays*. 3, portion of the central spike of a tassel; 4, a group of spikelets, such as often occurs instead of a pair; 5, spikelets on the lateral rachis of a tassel. Note that one spikelet of each pair is stalked, the other branched. (After Weatherwax.)

FIG. 588.—*Zea Mays*. Cross-section of lower part of a staminate spikelet of Country Gentleman sweet corn, × 20. *G*, glumes; *Lod*, lodicule; *F*, filament of stamen; *A*, anther; *L*, lemma; *P*, rudimentary pistil; *Pa*, palea. (After Weatherwax.)

(lemma and palea) may increase greatly in size. A lodicule has never been observed on the pistillate spikelet.

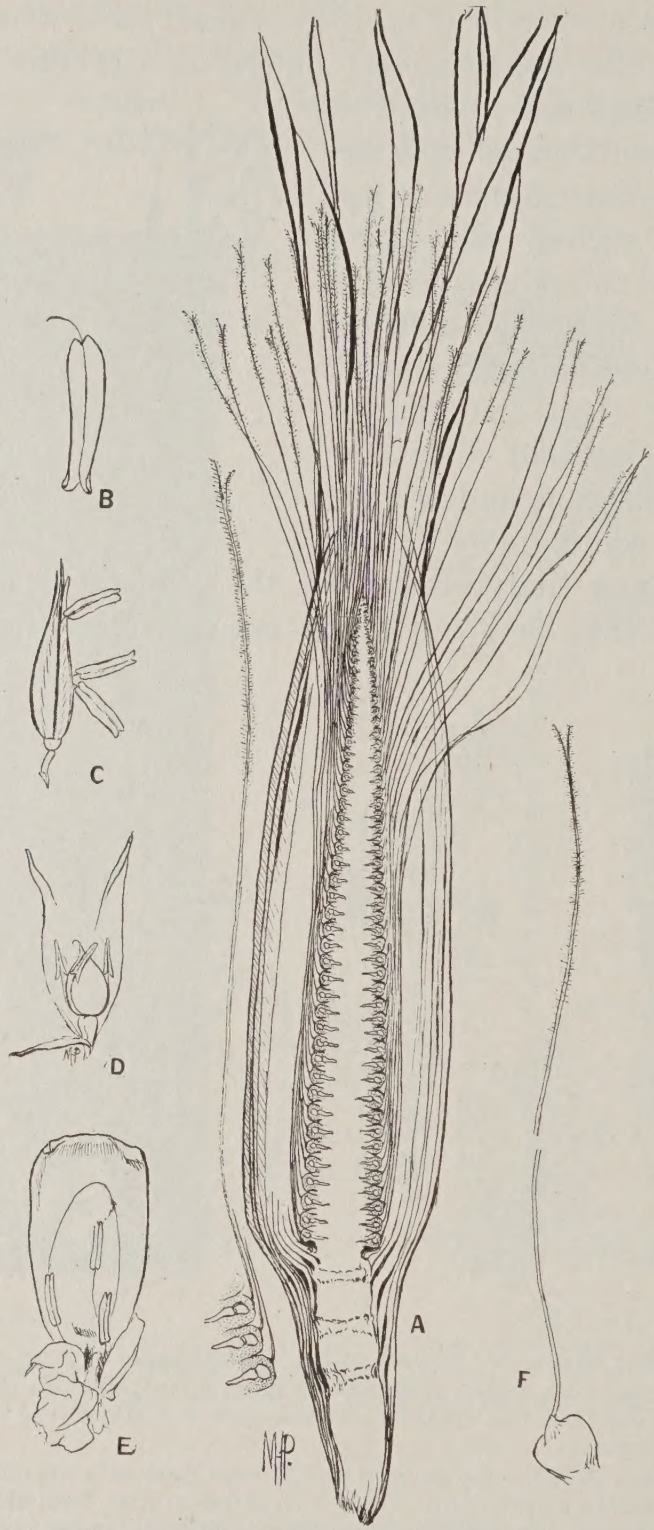


FIG. 589.—*A*, Pistillate spike ("ear") of *Zea Mays*, showing the attachment of silks to young "grains" (ovaries), all surrounded by external protective sheaths (husks) which are modified leaves; *B*, stamen, showing the lateral pores near the tip of the anther; *C*, staminate flower; *D*, a perfect flower from the tassel of pod corn; *E*, mature grain (ripened ovary), developed from a perfect flower, as shown by the three dried stamens which remain attached (redrawn from East); *F*, pistillate flower from a young ear.

Contrary to the case with the staminate flowers, the lower of the two pistillate flowers normally aborts. The bracts, however, do not abort; therefore each grain is surrounded by six bracts, three of which belong to the aborted flower.

The spikelets are also borne in pairs, each pair in a depression (*alveolus*) of the cob. The paired spikelets occur in double

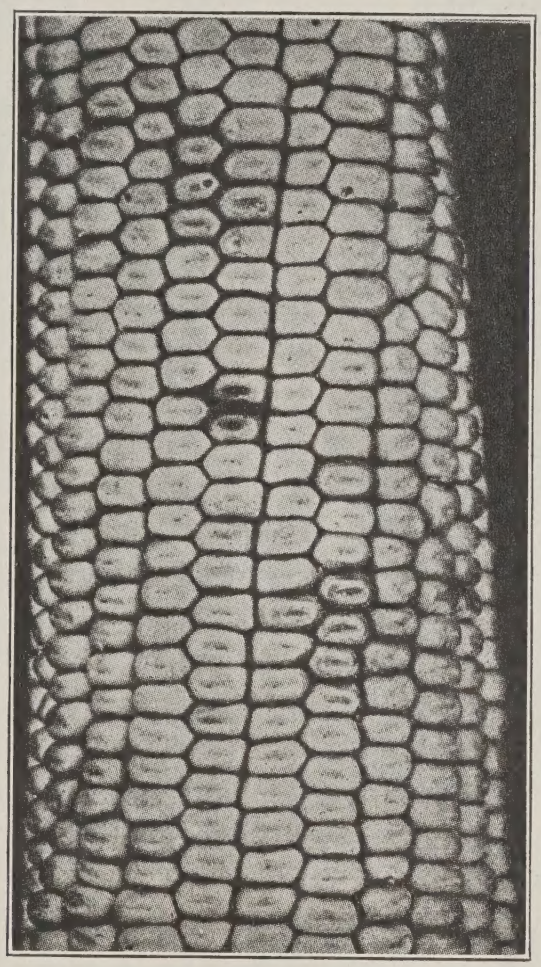


FIG. 590.—Portion of an ear of *Zea Mays*, showing the arrangement of the grains. Note that every second line of division between the rows is zig-zag, the alternating lines straight. The grains directly opposite each other on either side of a straight line of division were developed from the two spikelets of a pair. (After Kempton. U. S. Dept. Agr.)

rows lengthwise of the cob, alternating with the adjoining double pairs on either side. This explains the fact that every second line of division between the rows of grains is zig-zag, and the alternate lines are comparatively straight (Fig. 590).

The pistil comprises the basal *ovary* that matures into the *caryopsis* or grain, and the so-called silk. The silk has often been

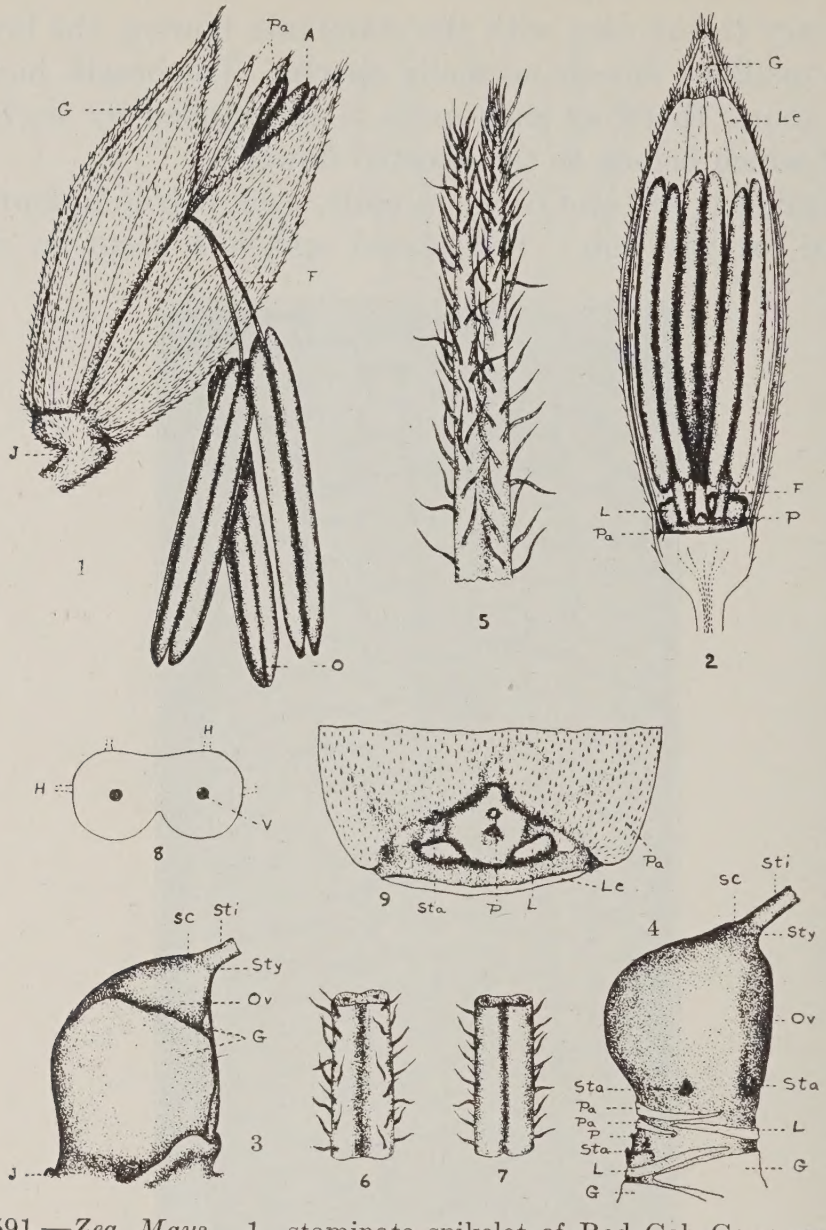


FIG. 591.—*Zea Mays.* 1, staminate spikelet of Red Cob Cory sweet corn, with one flower in anthesis. *G*, glume; *Pa*, palea; *A*, anther of unopened flower; *F*, elongated filament of mature stamen; *O*, lateral pore near tip of anther; *J*, joint of rachilla.

2, Staminate flower of same, with its own palea and the other half of the spikelet removed. *G*, glume; *Le*, lemma; *F*, short, thick filament of immature stamen; *P*, rudimentary pistil; *Pa*, base of palea that has been removed; *L*, lodicule.

3, Pistillate spikelet of same. *Sti*, stigma; *SC*, stylar canal; *Sty*, style; *Ov*, ovary; *G*, glumes; *J*, joint of rachilla.

4, Pistillate spikelet with glumes removed. *sta*, rudimentary stamen; *P*, pistil of aborted flower; *sta*, stamen of aborted flower; *G*, *L*, and *P*, scars left by removal of glumes, lemmae, and paleae, respectively.

5, End of stigma, showing two points at tip, and hairs which catch and hold the pollen grains in pollination.

6, Adaxial, and 7, abaxial sides of stigma a short distance from the style.

8, Cross-section of stigma, adaxial side above. *v*, vascular strands; *H*, places of attachment of hairs.

9, Aborted lower flower of pistillate spikelet. *Sta*, stamen; *P*, pistil; *L*, lodicule; *Pa*, palea; *Le*, scar left by removal of lemma. (All after Weatherwax. Legend slightly modified.)

interpreted as a long style, but Crozier[1] found that fertilization occurred when silks were pollinated after being cut off at various lengths, thus indicating that the silk is probably stigmatic throughout its entire length, and not at its forked apex alone. The longer the silks the longer the time required for fertilization, since the tip of the pollen-tube has to traverse a greater distance in growing down to the ovule. Silk will remain green and recep-

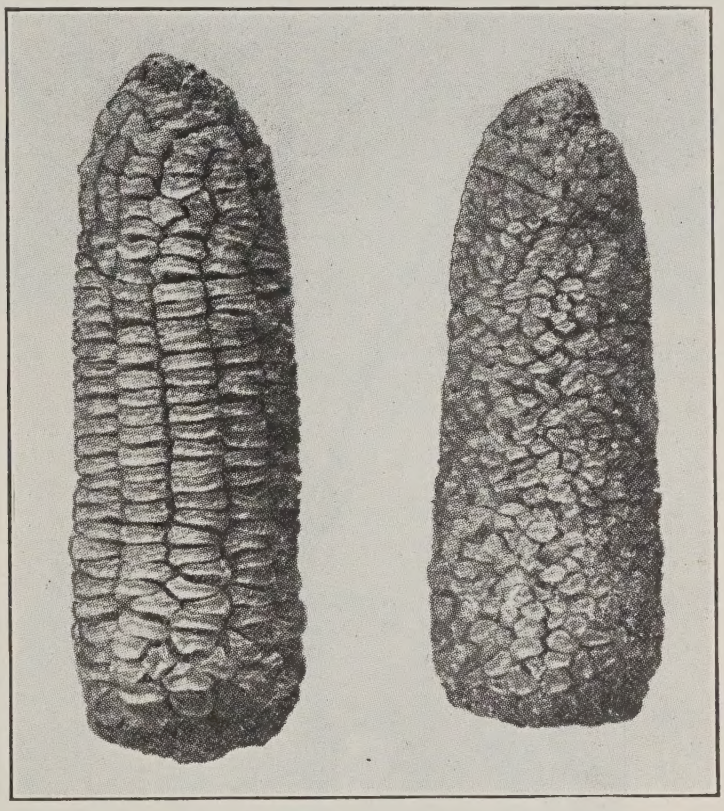


FIG. 592.—*Zea Mays.* Ears of Stowell's Evergreen (left), and of Country Gentleman (right), the latter showing irregular and crowded arrangement of the grains due to the development of both flowers in a spikelet, which doubles the number of grains. (After Weatherwax.)

tive and continue to grow in length for a time if not pollinated. In one such case Crozier measured silks that reached a length of 16 inches in 19 days. The silk is not cylindrical but asymmetrical in cross section, and its two-lobed character suggests that it should be interpreted as a compound stigma, formed by the fusion of two. The surface of the silk is covered with hairs which serve to catch and hold the pollen-grains (Fig. 591).

[1] Bot Gaz. **13**: 242. Sept., 1888.

If the silk is homologized as a stigma, then the style is the short projection at the apex of the ovary, just to one side of the silk. This projection is traversed by the so-called "stylar canal"

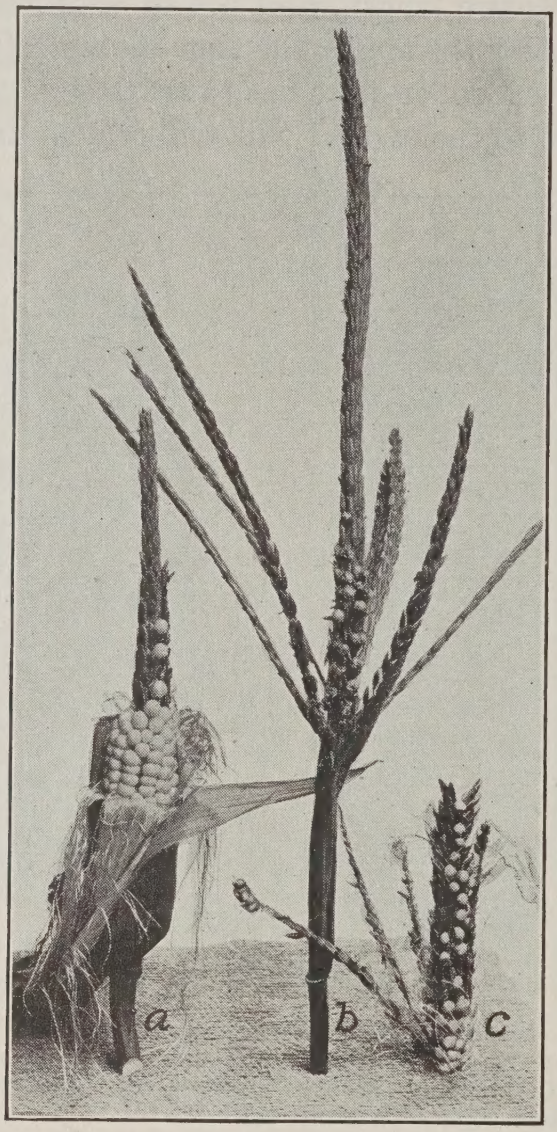


FIG. 593.—*Zea Mays*. *a*, Pistillate inflorescence (ear), showing normal pistillate flowers below, and perfect and staminate flowers above; *b*, staminate inflorescence (tassel), bearing some perfect flowers; *c*, portion of another staminate inflorescence bearing numerous perfect flowers.

(Fig. 597). Surrounding the pistil are the functionless rudiments of three stamens.

The lower pistillate flower is functionless in most varieties of corn, but both flowers have been found functional as a rule in the variety, Country Gentleman, so that the ear of this variety has

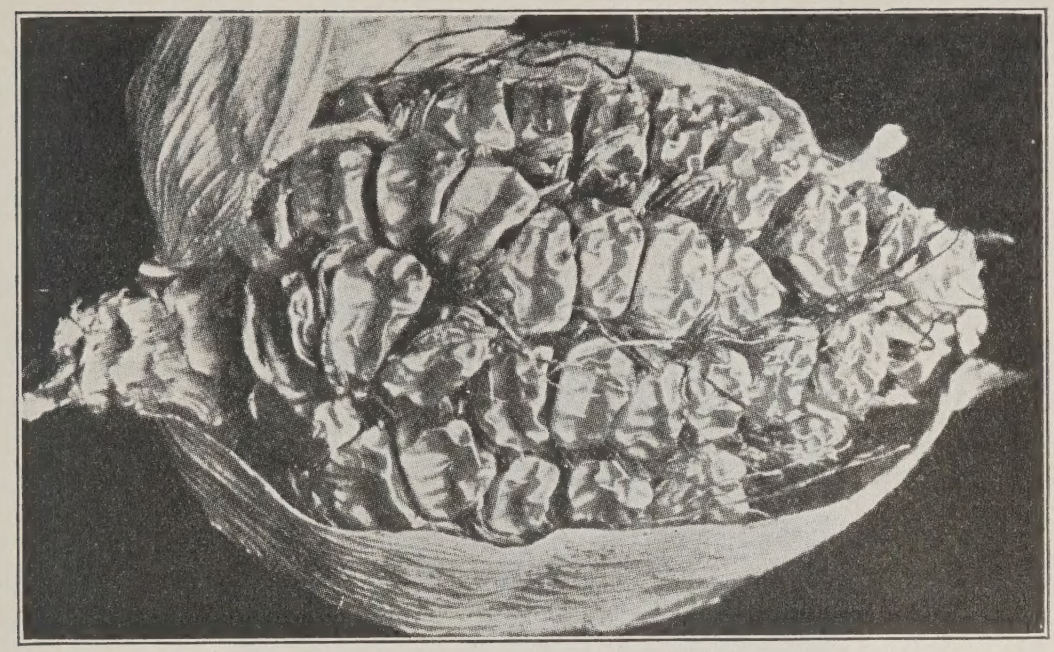


FIG. 594.—*Zea Mays.* Reversion to perfect flowers in an ear of corn. Note the stamens around the grains. (After East.)

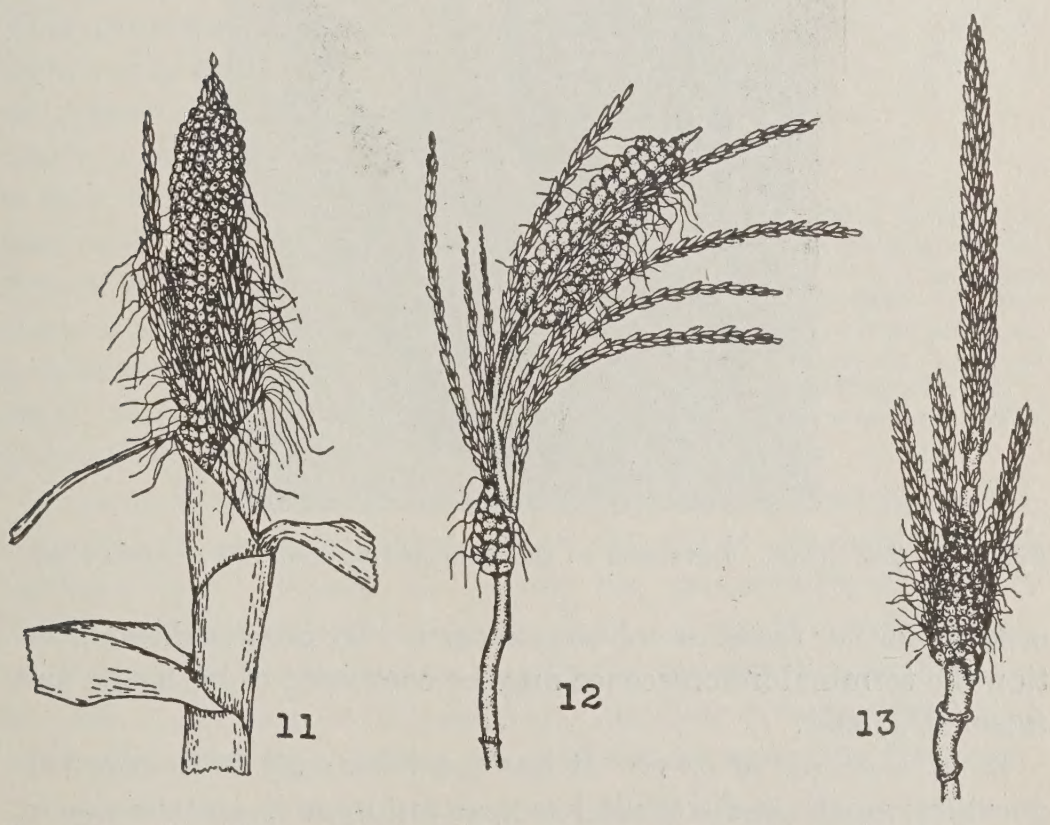


FIG. 595.—*Zea Mays.* Terminal inflorescences of suckers, bearing both ears and tassel. (After Weatherwax.)

twice as many grains as some other varieties. This results in crowding, and the abnormally long and slender grains do not appear to be arranged in rows (Fig. 592).

Abnormal inflorescences are not infrequently met with, having grains (pistillate or perfect flowers) on the tassel, and staminate or perfect flowers on the cob (Figs. 593 and 594). Perfect flowers

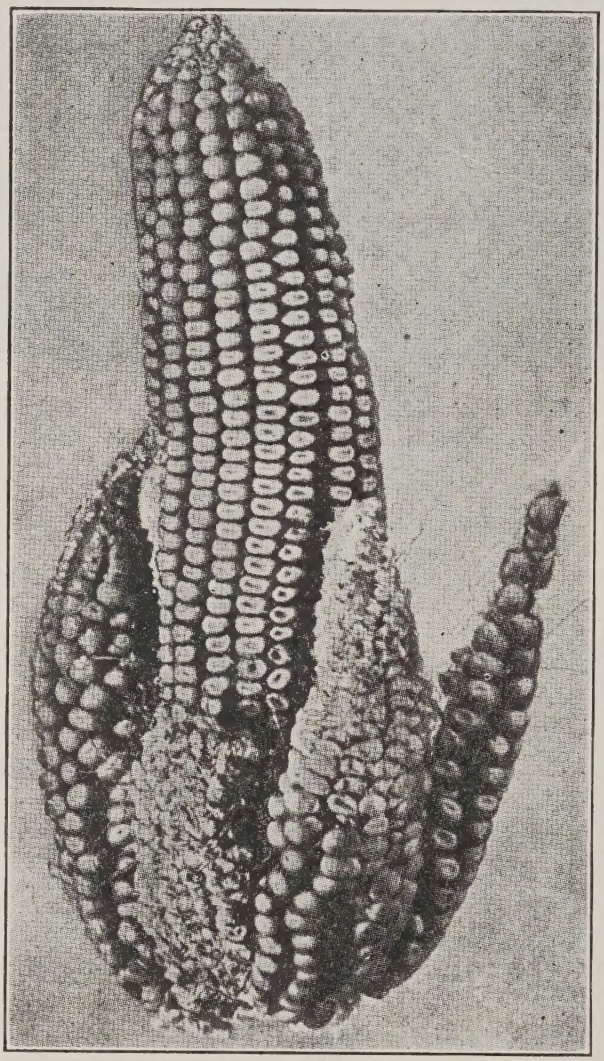


FIG. 596.—*Zea Mays.* Reversion to the branched type of ear. (After East.)

occur on either tassel or cob in pod corn. By greater differentiation the terminal inflorescence may be composed of both ears and tassel (Fig.595).

What is an ear of corn? It has not been easy to answer this question; much careful study has been put upon it, and the weight of evidence seems to indicate that the ear is the homologue of the

central spike of the tassel. "Every part of either can be identified in the other, and they bear identical relations to the other parts of the shoots which they terminate." The apparent difference between the two results from the different manner in which they develop. Abnormal inflorescences, especially of suckers (Fig. 595), afford some of the strongest evidence that this is the correct interpretation of the ear.[1] Additional evidence is found in the not uncommon reversions to a branched type of ear (Fig. 596).

Pollination is accomplished by the wind and by gravity. The staminate flowers open largely as a result of the pressure of the elongating stamens. The pollen is shed from a small opening which is located, not at the tip of the stamen, but on the side just above the tip (Fig. 591). This prevents the pollen grains from easily falling out when the air is quiet, but allows them to be easily shaken out when the wind is blowing and when, therefore, they are more apt to be widely disseminated. This reduces the chances of their falling directly downward on the silk of the same plant, and helps to insure cross-pollination.

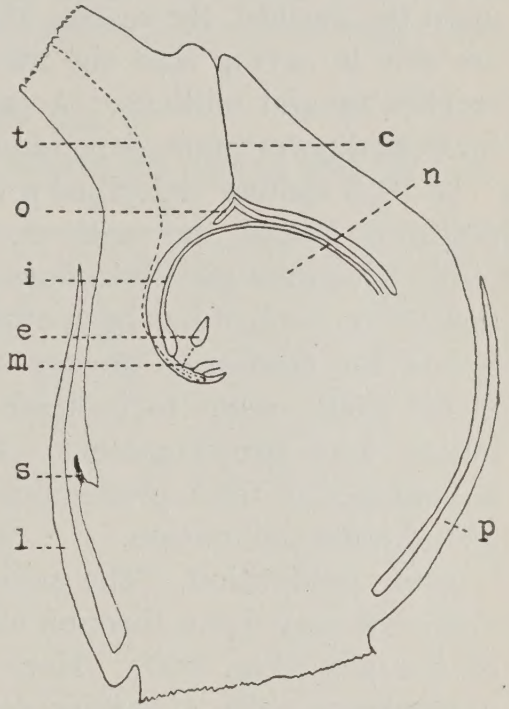


FIG. 597.—*Zea Mays*. Diagram of longitudinal section of pistillate floret, greatly enlarged. *l*, lemma; *p*, palea; *e*, embryo-sac; *n*, nucellus; *o*, outer integument; *i*, inner integument; *m*, micropyle; *c*, stylar canal; *t*, course of pollen-tube after reaching the ovary; *s*, rudimentary stamen. (After Weatherwax.)

Cross-pollination is further assured by the fact that the staminate flowers normally mature before the silk is out and receptive (proterandry). Nearly all grasses are proterandrous Pollen is best disseminated on dry, bright days. A condition of drought, while favoring the scattering of pollen, delays the development of the silk; under such conditions many pistillate flowers will not get pollinated, and the mature cob will not be perfectly filled out.

[1] Another theory is that the ear results from the fusion of several pistillate spikes of two rows each.

Under average conditions a large amount of self-pollination results.

Estimates of the amount of pollen produced by maize vary widely, one authority giving 9000 pollen grains for every ovule (on the basis of 2000 ovules to a plant), another 45,000 grains for each ovule (for Dent corn). The total number of pollen grains has been estimated at from 18,000,000 to 50,000,000, depending upon the variety, the season, the locality, and the observer. We are safe in saying that the number is very large, and probably reaches several millions. A tassel may continue to shed pollen for 6–10 days or more, depending largely on the weather.

In 1913 Collins[1] described a variety of maize in which the silks matured before the anthers, thus resulting in *proterogyny*.[2] Now, whenever pistillate flowers occur on a tassel, or staminate flowers on a cob, it has been observed that the silks usually mature before the staminate flowers open. This (together with other facts) would seem to indicate that the primitive ancestors of maize were proterogynous. Proterogyny is considered more advantageous than proterandry, as tending more certainly to insure cross-pollination.

After pollination, "the pollen tube emerges very soon and makes its way down through one of the stigma-hairs to the body of the silk (Fig. 600). Here it pushes its way between the parenchyma cells, absorbing food from them, no doubt, until it reaches one of the vascular bundles, which it follows toward the ovary."

"At the time of its emergence from the pollen grain the tube is greatly exposed to dessication, and this continues until it has made its way into the body of the silk. This, together with the fact that the pollen grains themselves dry up very readily and are seldom viable for more than a day or two, probably accounts for the importance to the corn crop of warm rains at the time of pollination."[3] (*Cf.* Fig. 598.)

[1] Collins, G. N. A variety of maize with silks maturing before the tassels. U. S. Dept. Agr. Bur. Plant Ind. Circular No. 107. Washington, D. C., 1913.

[2] This variety was raised from seeds obtained at Granada, Spain, in 1912 by Mr. Walter T. Swingle of the U. S. Bureau of Plant Industry, and planted at Lanham, Maryland.

[3] Weatherwax, Paul. Gametogenesis and fecundation in Zea Mays, etc. Bull. Torrey Bot. Club. **46**: 77. March, 1919.

The structure of the pistillate floret at the time of pollination is shown in longitudinal section in figure 597. The ovule, which nearly fills the cavity of the ovary, has an outer and an inner integument. The micropyle leads to the *embryo-sac*, the structure of which, at a late stage of its development, is shown at 12, figure 599. There are 8 nuclei, four at each end. As the embryo-sac matures, two of these nuclei, the *polar nuclei* come together and fuse, forming the primary endosperm-nucleus (13, *p*,

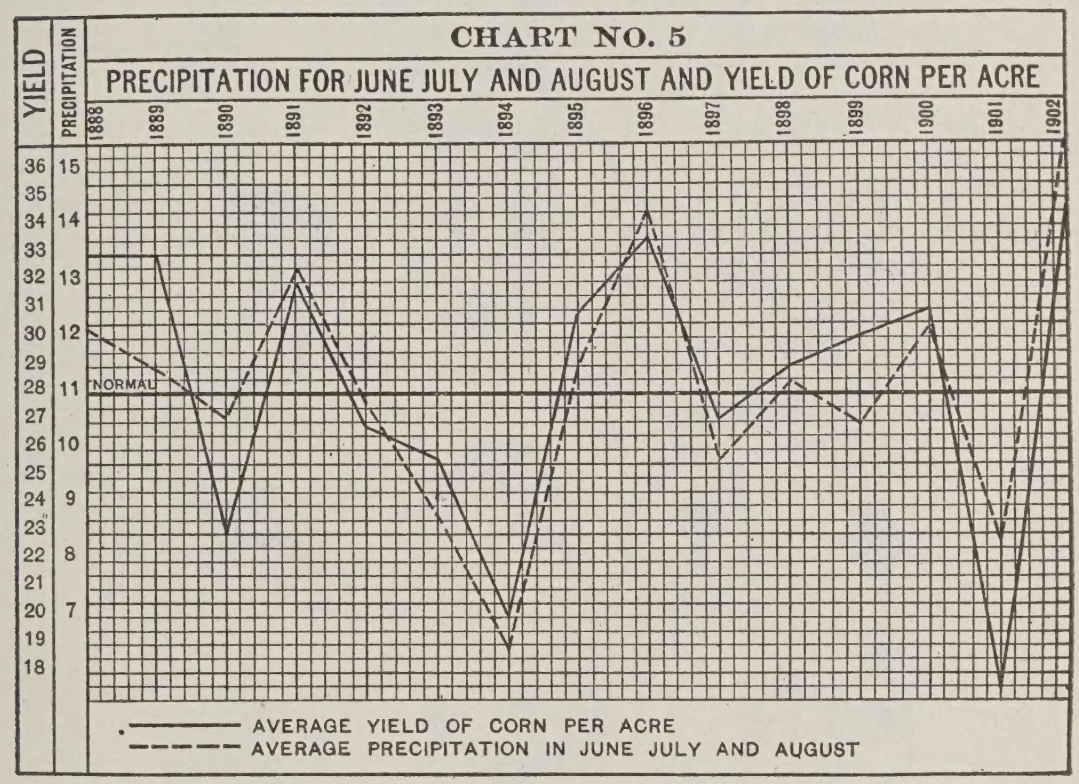


FIG. 598.—*Zea Mays.* Relation between precipitation for June, July, and August and yield of corn per acre, through a period of 14 years (1888–1902), in the States of Ohio, Indiana, Illinois, Iowa, Nebraska, Kansas, Missouri, and Kentucky. (After J. Warren Smith, U. S. Dept. Agr. Year Book, 1903.)

Fig. 600). At the end nearest the micropyle one of the remaining nuclei becomes the nucleus of an *egg-cell*, while the other two become the nuclei, respectively, of two other cells, known as the helpers, or *synergids*. At the opposite end of the embryo-sac the three *antipodal cells* have undergone division, forming the several celled antipodal tissue which is found in the embryo-sacs of most grasses.

The sperm-cells or *sperms*, formed in the pollen-grains before the anthers dehisce, pass down the pollen-tube and out into the

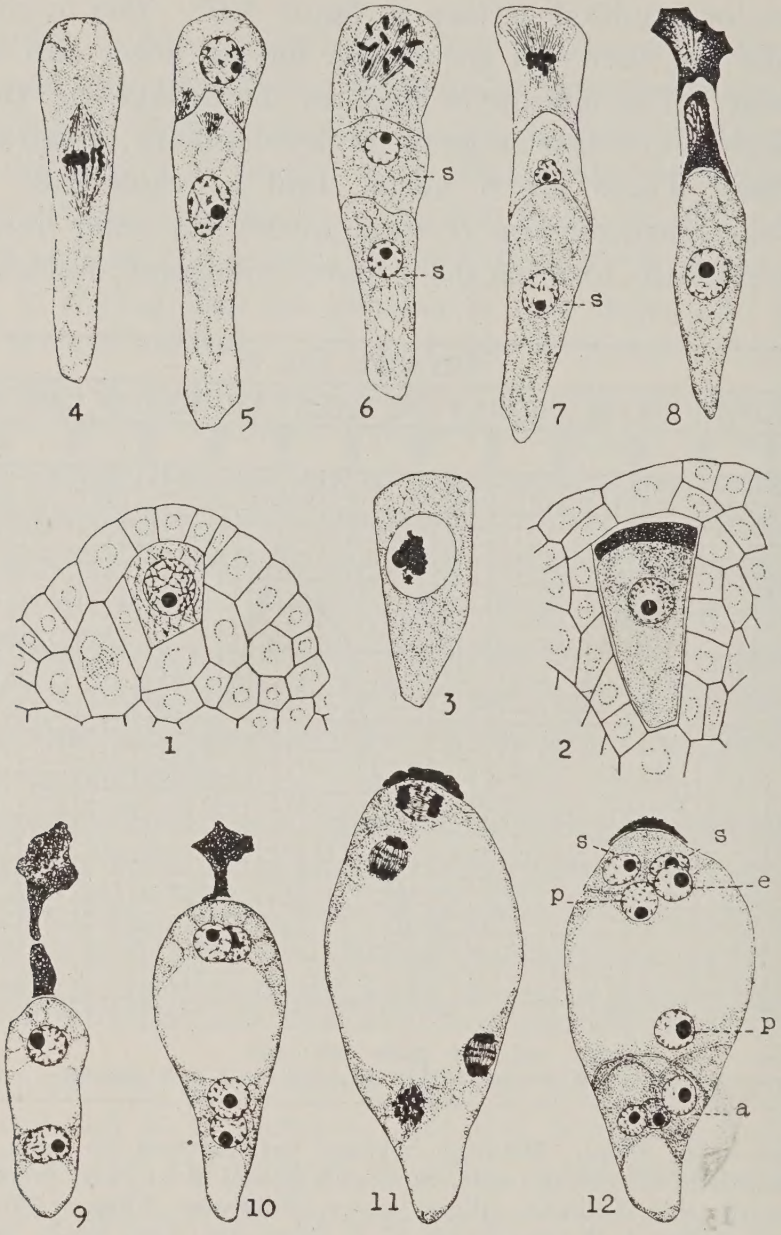


FIG. 599.—*Zea Mays.* Origin and structure of embryo-sac. 1, archesporial cell; 2, megaspore-mother-cell and disorganized tapetal cell; 3, megaspore-mother-cell with nucleus in synapsis; 4, first nuclear division of megaspore-mother-cell, involving chromosome reduction (heterotypic division); 5, daughter-cells; 6, two megaspores resulting from division of one daughter cell, and the second (micropylar) daughter-cell in process of division; 7, the dividing daughter-cell and one megaspore are beginning to disintegrate; *s*, functional megaspore; 8, functional megaspore absorbing the other three and enlarging; 9–12, steps in the germination of the megaspore and the organization of the embryo-sac; *s*, synergids; *e*, egg-nucleus; *p*, polar nuclei; *a*, antipodal cells. (After Weather' wax.)

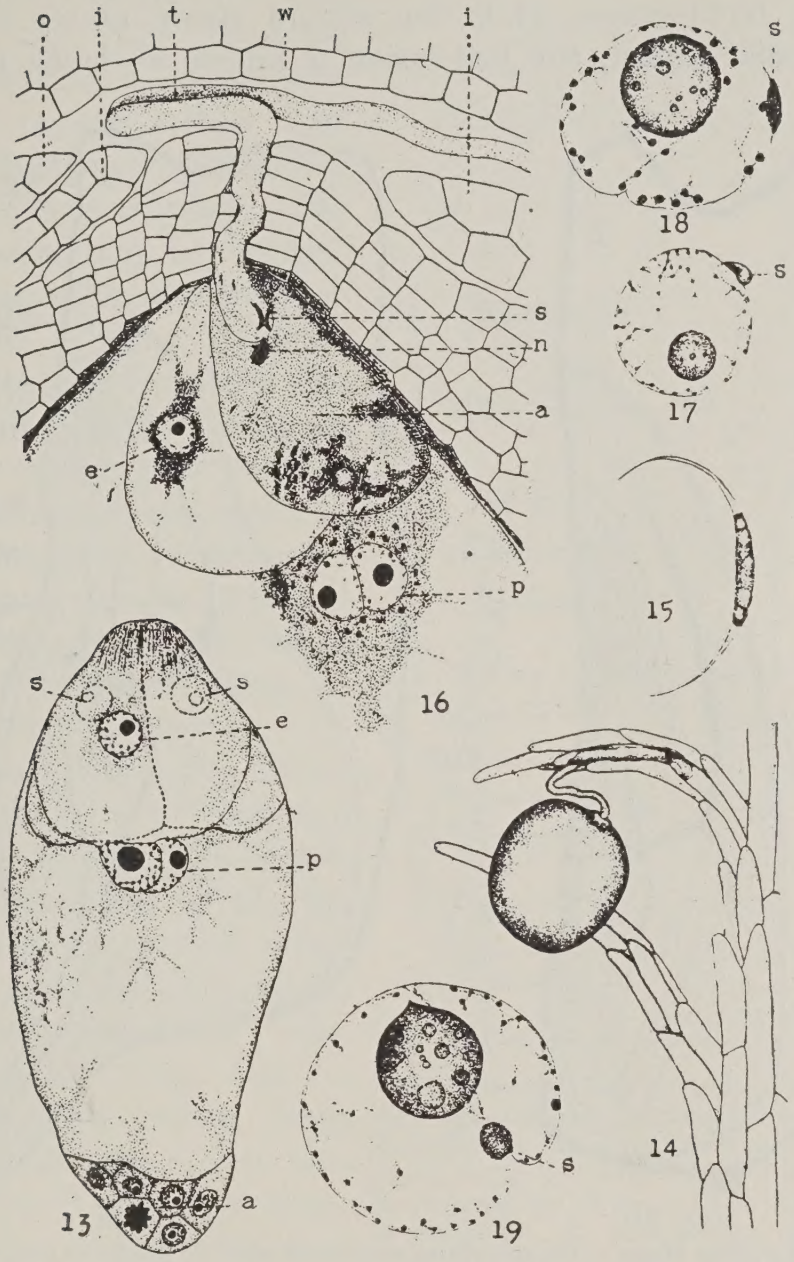


FIG. 600.—*Zea Mays*. 13, embryo-sac soon after organization; *s*, synergids (position shown by dotted lines); *e*, egg-nucleus; *p*, polar nuclei; *a*, antipodal tissue. 14, pollen-grain germinating on stigma-hairs. 15, sperm from pollen-grain. 16, pollen-tube entering embryo-sac; *o*, outer integument; *i*, integument; *t*, pollen-tube; *w*, wall of ovary; *s*, sperms; *n*, tube-nucleus (probably); *e*, egg-nucleus; *p*, polar nuclei in contact; *a*, one synergid; other synergid not shown. 17, sperm-nucleus, *s*, in contact with egg-nucleus. 18, 19, sperm-nuclei, *s*, in contact with the fusing polar nuclei. (After Weatherwax.)

embryo-sac. One of them fuses with the egg-cell, thus accomplishing fertilization, while the second sperm unites with the fusing polar nuclei; this last fusion is known as *double fertiliza-*

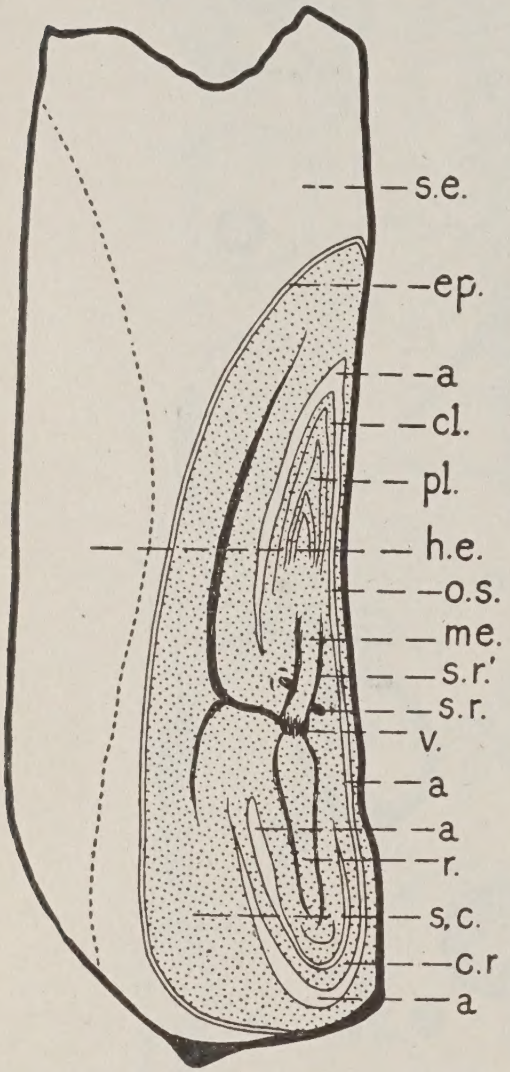


Fig. 601.

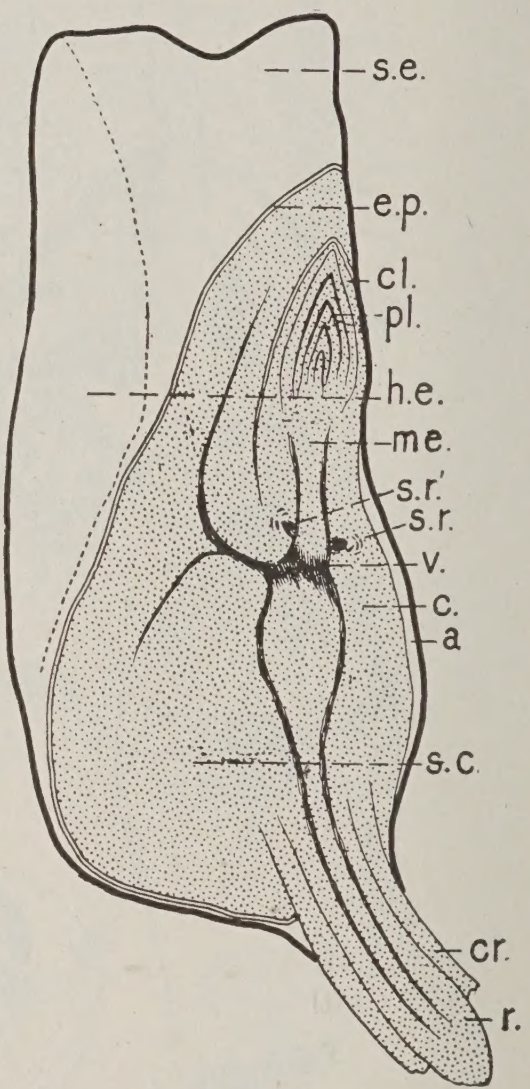


Fig. 602.

Fig. 601.—*Zea Mays.* Longitudinal section of mature grain of corn, showing the parts of the embryo. *h.e.*, horny endosperm; *s.e.*, starchy endosperm; *sc.*, scutellum; *ep.*, epithelium; *cr.*, coleorhiza; *r.*, radicle; *s.r.* and *s.r.'*, initials of secondary radicles; *v.*, vascular tissue; *cl.*, coleoptile; *pl.*, plumule; *me.*, mesocotyl; *a.*, air spaces between tissues in the grain; *o.s.*, scutellum overlapping face of embryo. × 5. (After Toole.)

Fig. 602.—*Zea Mays.* Longitudinal section of grain after about 48 hours' germination. *c.*, cortical tissue which greatly enlarges in germination; other letters as in Fig. 601. (After Toole.)

tion. Weatherwax found that fertilization is accomplished in about 24 hrs. after pollination (Fig. 600).

The fertilized egg (oösperm) develops into the *embryo* of the corn-grain (Figs. 601 and 602), but the fertilized fusion nucleus develops much more rapidly than the oösperm, and forms the *endosperm* of the corn grain. The endosperm may be "sweet" or "starchy"; if starchy, it may be "horny" (corneous) and translucent, or soft and white, the predominance of one or the other of these characteristics, giving rise to *pop*, *flint*, *soft*, and *dent* corn. The mature grains of sweet-corn always wrinkle when dried, due to shrinkage of the sugary endosperm.

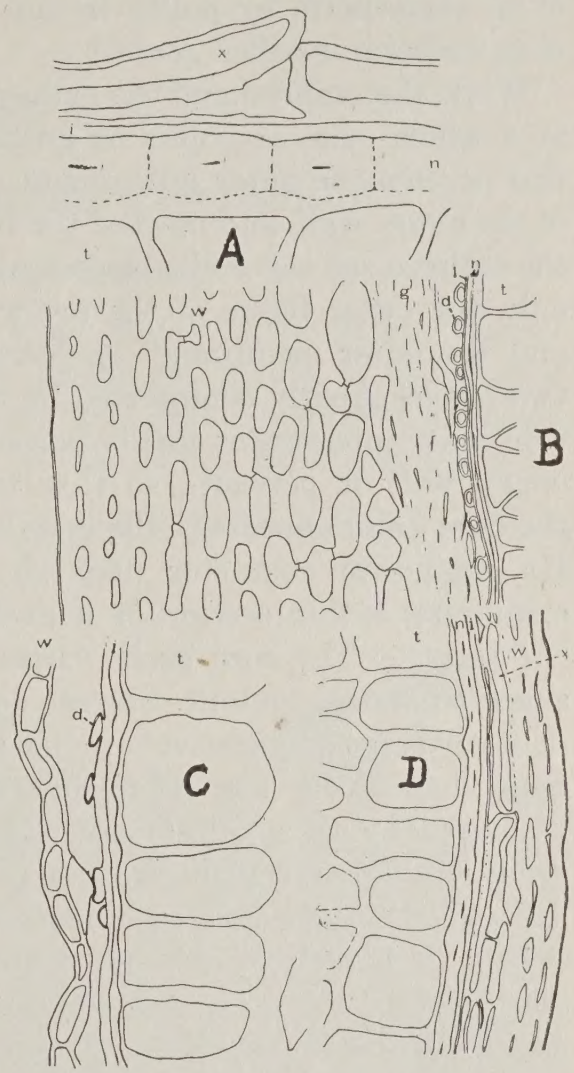


FIG. 603.—*A*, cross-section of the inner layers of the coat of the mature wheat grain, showing the union of the chlorophyll cells of the ovary wall with the inner integument. *B*, cross-section of the coats of the corn grain at maturity. *C*, cross-section of the coats of the mature oat grain, showing the union of the remaining cells of the ovary wall with the inner integument. The layer to the left of *i* is the inner integument; to the right, the epidermis of the nucellus. *D*, cross-section of the coverings of the mature wheat grain. *d*, inner epidermis of ovary wall; *g*, line of compacting of cells in ovary wall; *i*, inner integument of ovule; *n*, nucellus; *t*, endosperm; *w*, wall of ovary; *x*, chlorophyll-bearing layer of ovary wall. (After R. H. True.)

Xenia.—When the second sperm unites with the fusion nucleus we see that hereditary characters from the staminate parent are introduced into the composition of the endosperm cells. Now when sweet corn is crossed with pollen from a starchy variety the "starchy" character dominates (*i.e.*, is *dominant*) over sweetness, and the grains of the hybrid are starchy. We see now that the explanation of this is found in the phenomenon of double-fertilization, by which the factors that make for the dominant character of starchiness are introduced into the hereditary composition of the

cells of the endosperm. Any effect produced on the endosperm of an angiosperm by pollen from a plant having a different kind of endosperm is called *xenia.*[1]

While the embryo and the endosperm are developing, the fruit as a whole—the caryopsis or grain—is also maturing. During this process the outer integument of the ovule, the inner tissue of the ovary wall, and most of the tissue of the nucellus (in which the embryo-sac was embedded) are absorbed, leaving at maturity only the outer tissue of the ovary wall, the inner integument, and the outer membrane (epidermis) of the nucellus—the last two tissues greatly compressed by the growth of adjacent tissue. The inner integument finally becomes fused with the cells of the ovary wall or pericarp, so that the outer covering or skin of the corn grain appears to the unaided eye as a simple membrane. Its composite character may be demonstrated, however, by examining a thin section of it under the microscope (Fig. 603).

Popcorn.—The corn grain varies widely in the proportion of sugar to starch content. Sweet corn, as its name implies, and dent corn are comparatively rich in sugar. Popcorn, on the other hand, has a very low sugar content. The popping of popcorn is caused by the explosion of the starch grains. Each starch grain contains a certain amount of moisture, which varies with age and with the conditions under which the corn has been stored. When the kernels of corn are heated to a temperature of about 350°–400° F. in two to three minutes the moisture *in the starch grain* is turned into steam. When the steam pressure has reached a certain point it ruptures the starch grain. The starch is hydrolyzed, and all traces of cellular structure in the embryo and endosperm are destroyed. Various "puffed" breakfast foods are produced by heating cereal grains under pressure; when the pressure is suddenly released, the grains explode. This process was discovered while studying the structure of starch grains in a botanical laboratory.

More than 100 commercial products are made from corn grains, including corn-starch, sugar, syrup (karo), oil, and bone-black. There is also extracted from the embryo a gum from which the red "rubber-sponges" and eraser tips for lead pencils may be made.

[1] The term *xenia* is from the Greek word ξένια (*xenia*), gifts of friendship, from ξένος (*xenos*), strange.

CHAPTER XXXVIII

MONOCOTYLEDONS (CONTINUED)

ORDER, Palmales

This order contains only the one family of the palms (*Palmaceae*). These are exceedingly important plants in the tropics and sub-tropics, yielding not only food (dates, coconuts, cabbage-palm, etc.), but also leaves for thatching roofs and for fans,

FIG. 604.—Cottage of Cuban farmer. The roof is thatched with the leaves of the Royal and Barrigona palms (*Roystonea regia* and *Colpothrinax Wrightii*). The walls are from the caudices of Royal Palm. The palms with caudices swollen near the base are Barrigonas, and these stems, including the swollen portion, are frequently used as porch pillars in the rural sections of Cuba.

timber for construction (Fig. 604), sugar and wine (Coconut palm, and *Arenga saccharifera*), oil (*Elaeis guineensis*—The African Oil-palm), "vegetable ivory" (the horny endosperm of the seeds of *Phytelephas*[1] *macrocarpa*), sago (from the stem-pith of the

[1] Phytelephas = "elephant plant," from the Greek, φῡτόν (phyton), *a plant* + ἐλέφας (elephas), *elephant*, the elephant's tusks being the source of real ivory.

Sago palms (*Metroxylon* Sps.), and also from *Caryota Urens*, *Phoenix farinifera*, and others. The leaf-epidermis of a Madagascar palm (*Raphia Ruffia*) forms the "raffia" so extensively used by horticulturists and others. The terminal bud of *Roystonea oleracea*[1] and other palms, commonly known as "cabbage palms," is used for food, but the gathering of it, of course, kills the palm. The *rattan* of commerce is largely the creeping or climbing stem of the palms, *Calamus* and *Daemonorops*. As many as fifty other species are less important sources. Most of the rattans come from the Malay Archipelago. They are sometimes more than 200 yards long, thus being among the longest of known plants.

There are from 1000–1200 known species of palms, and the Palm family is second only to the Gramineae in economic importance.

Palms have a fibrous root-system and possess a wide range of adaptation to soil conditions, some, like the coconut, preferring much moisture and nearness to the sea, others thriving on comparatively dry rocky ledges. The stem or trunk is usually not branched, but rare exceptions to this are known. The crown of leaves is confined to the upper end of the stem, the older leaves falling off as the stem grows in length. In some species the leaf-stalk breaks off at the trunk, leaving only a leaf-scar; in other cases the abscission layer is some distance up from the leaf-base, so that the lower portion remains on the trunk after the leaf is shed.

The leaves may be divided palmately (Palmetto, Coconut Palm, etc.), or pinnately (Date Palm).

The inflorescence may be a *spike*, or branched to form a *panicle*. There are usually several spathes. The inflorescences (usually axillary) hang down below the crown of leaves; when they are terminal the tree dies after flowering and fruiting. The flowers are of the typical monocotyledonous type, with three sepals, three petals, six stamens (one opposite each sepal and petal), and a pistil of (almost always) three carpels either separate or united to form a compound pistil. The fruit varies greatly, morphologically, according to the species, being usually a

[1] The same as the specific name of the cabbage (*Brassica oleracea*), which see (p. 608).

FIG. 605.—Coconut Palm (*Cocos nucifera*). Tree in Ceylon. (From Bull. Agricole du Congo Belge. 1910.)

berry or a drupe. In the latter case there is a smooth or scaly *epicarp*, a fleshy, or fibrous *sarcocarp*, and a bony, woody, or

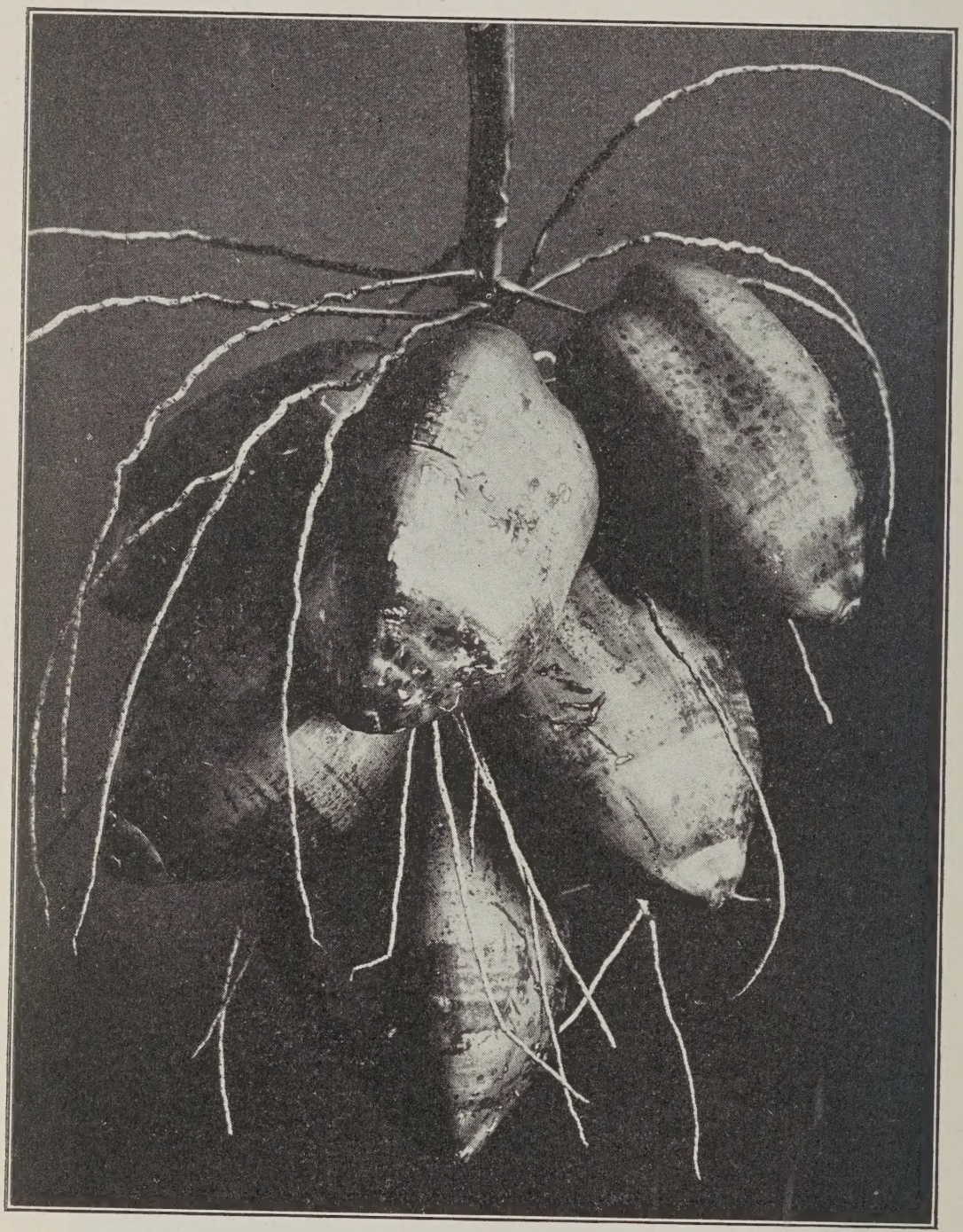


FIG. 606.—Coconut Palm (*Cocos nucifera*). Stalk of inflorescence bearing a number of coconuts and sterile pedicels. Grown near Miami, Florida.

fibrous, *endocarp*. The single seed is erect or pendulous, the seed-coat (*testa*) usually adhering to the endocarp, the endosperm

abundant, and the embryo very small in proportion to the bulk of the entire seed.

The palms are either dioecious (*e.g.*, Date Palm), or monoecious (*e.g.*, Coconut and Royal Palms), or rarely polygamous. The Palmetto (*Sabal palmetto*) and other species of *Sabal*, and some other genera have perfect flowers. Pollination is accomplished by the wind.

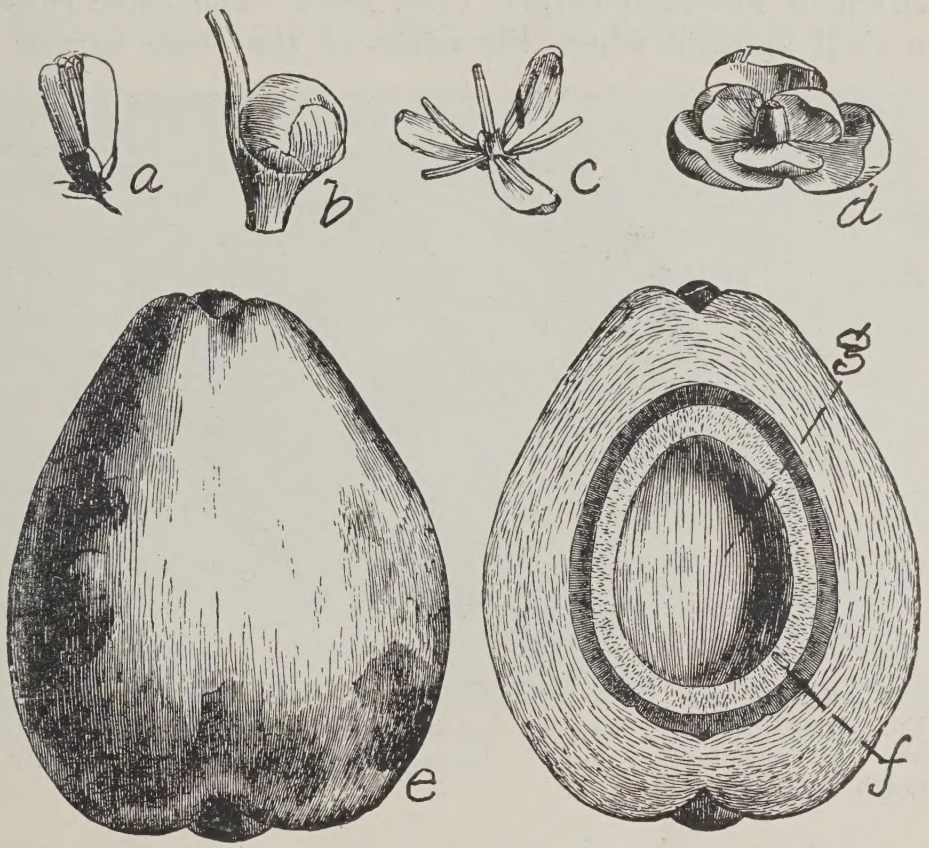


FIG. 607.—*Cocos nucifera*. *a*, staminate flower-bud; *b*, pistillate flower-bud; *c*, staminate flower; *d*, pistillate flower; *e*, fruit; *f*, embryo, embedded in fruit ("meat") in longitudinal section; *g*, cavity in the hard endosperm which contains the milk (soft endosperm). (After Baillon, modified.)

THE COCONUT PALM

The Coconut Palm (*Cocos nucifera*) (Fig. 605) is said to have a greater number of uses than any other tropical tree, and from that point of view is the most important of all the species of palms. Its leaves are used for thatching, its stem has various uses, the juice of the inflorescence forms, when fermented, an alcoholic drink, the fibers of the husk (*mesocarp*) are used in the manufacture of door mats, ropes, brushes, and other articles,

the empty shell (*endocarp*) is used as a vessel to hold liquid, the white fatty "meat" is eaten, or used as a source of coconut-oil, and the "milk" is highly prized as a drink. The fruit (Fig. 607) is a large *drupe* containing one seed; the exocarp (husk) is usually removed before shipment to northern markets. The three conspicuous spots or "eyes" at one end of the fruit are the "germination pores" of the original carpels—two representing the aborted or absorbed carpels (Fig. 608). The three ridges on the shell indicate where the edges of the three carpels met.

FIG. 608.—End of a coconut with the husk removed, showing the three "eyes" or "germination pores." In germination the seedling usually grows through the larger pore.

Under the germination pore of the fertile carpel is the micropyle of the seed.

The white meat and the watery milk together constitute the endosperm, the embryo being imbedded in the hard endosperm just underneath the germination pore of the fertile carpel (Fig. 607). When the seed germinates (Fig. 609) the embryo grows out through the germination pore. Notwithstanding its hard shell, thick husk, and large size, the coconut is one of the most delicate of seeds, physiologically speaking. It remains viable only about one month after it becomes ripe. Moreover it is easily injured by bruising, so that in the East Indies seeds intended for planting are picked by hand and lowered carefully

to the ground by ropes. Seeds bruised by falling to the ground, or otherwise, will either not germinate at all, or will produce only weak seedlings. The thick husk may afford some slight protection in this connection, but even if the husk only is bruised, decay may set in and destroy the power of germination.[1] If the seeds are kept where it is too moist, too dry, or too hot (*e.g.*, exposed too long to the tropical sun) they will fail to germinate when planted. The seedlings will not stand excessive shading, and are easily choked out in competition with other vegetation.

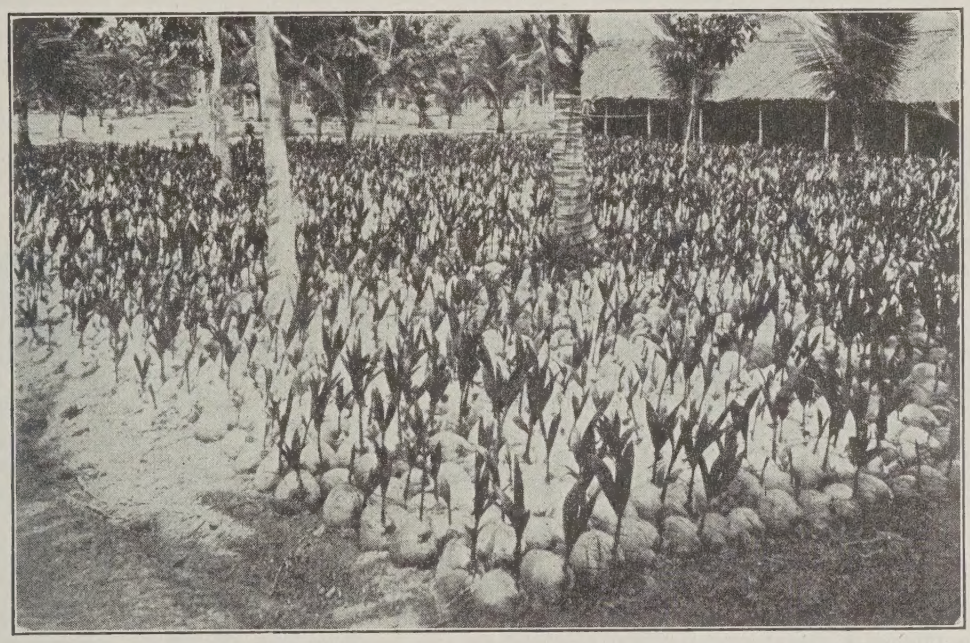


FIG. 609.—Germinating coconuts. (From Bull. Agricole du Congo Belge, 1910.)

In America only one variety is generally recognized, but in the Malay Archipelago there are as many as 50 varieties, resulting from artificial selection and differing in amount or quality of milk or oil, flavor of the "meat," quality of the fiber, or other characters.

Contrary to common opinion, the growth of wild coconut palms is not confined to coastal regions nor to sea level. They are found in both the old and new world 100–200 miles inland, and in the Hindostan Peninsula they flourish at an elevation of nearly 3000 feet above sea level.

[1] Cook, O. F. The origin and distribution of the cocoa palm. Contrib. U. S. Nat. Herbarium. **7**: 257–293. Washington, 1901.

In the Philippine Islands, where there is no train service to most of the interior of the country, coconuts grown inland are stacked on large rafts and floated down the rivers, somewhat as logs are transported in America. (Fig. 610.)

The native home of the coconut is not positively known. Various writers have advanced arguments in favor of its origin in the old world and in particular in the East Indian Archipelago, while others, and in particular O. F. Cook, have adduced evidence of its

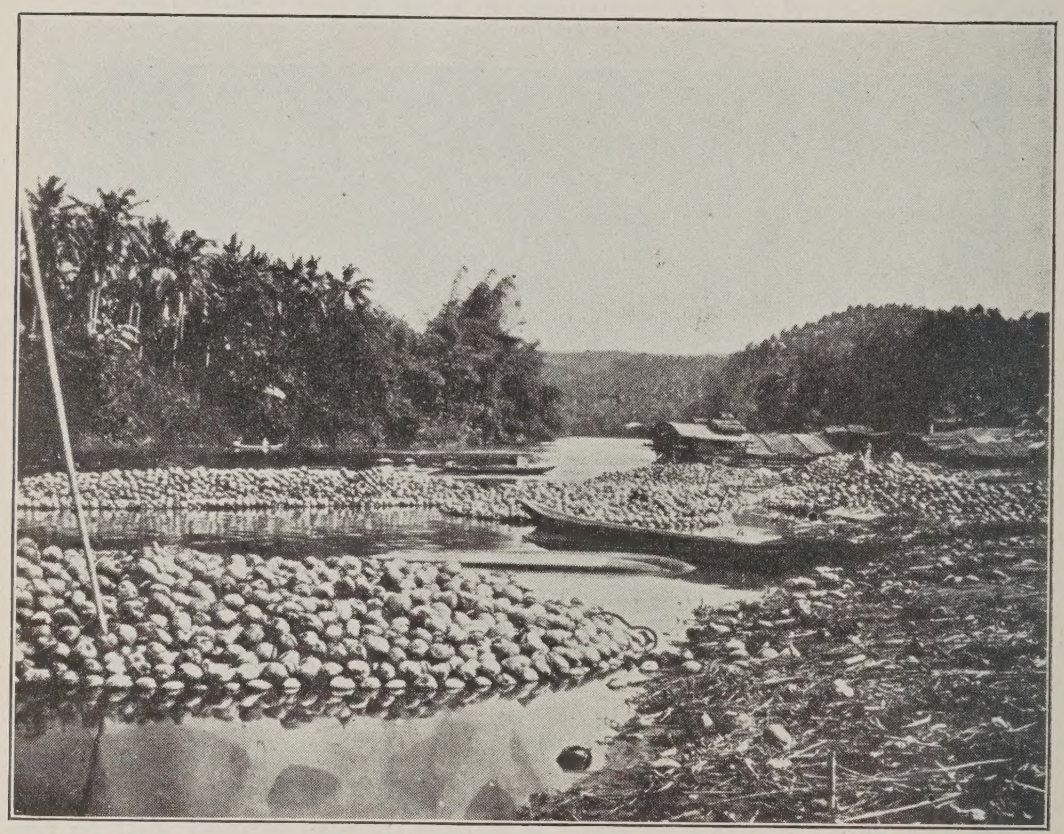


FIG. 610.—Transportation of coconuts by raft in the Philippine Islands. (Publishers Photo Service, Manila.)

origin in South America. Cook notes that all of the 20 genera most closely related to *Cocos* (and grouped by him in one family, *Cocaceae*), with some 200 species are strictly American, with the single exception of *Elaeis*, the African Oil-palm (*Elaeis guineensis*), of which, one species is, as the name indicates, African. Considering this and the fact that no other genus or species of palms is common to both America and Asia or Polynesia, and in view of a mass of other evidence, Cook concludes that its Asiatic origin is highly improbable.

In the case of the tall coconut (in Ceylon), a period of 3½ to 5 weeks, according to Petch, is required for all the staminate flowers on a given tree to open. A period of 2 to 5 days then elapses before the pistillate flowers on the same tree begin to open, and they are all opened in a period of from one to seven days, varying with the number of pistillate flowers. This makes cross-pollination the rule and it is accomplished by insects (notably bees and hornets) and by the wind. Jack and Sands, however, state that, "In the warm, humid atmosphere of the lowlands of Malaya cocoanuts appear to behave differently. The length of duration of the male phase is curtailed, while the duration of the female phase would appear to be longer on both tall and dwarf trees; but the most striking difference is the fact that in Malaya the female phase not only begins, but most frequently ends before, or at the same time as, the male phase, thus rendering self-pollination the rule instead of being an occasional chance occurrence."[1]

THE DATE-PALM

The date-palm, *Phoenix dactylifera*[2] (Fig. 611), is hardly second to the coconut palm in importance. It has been known and utilized by man from prehistoric times, and Strabo, referring to the use of the date by the ancient Babylonians, says that all their wants, not supplied by grain, were supplied by the date palm. In addition to the palms providing shade for fruit trees and vegetable crops, and in addition to the use of their fruit as food, the dates, soaked in water in fermenting vats, are used to prepare an alcoholic beverage. Date syrup and vinegar are also made from the fruit. In Arabia and northern Africa ground date stones are fed to camels and other stock, they are strung together for necklaces, and are also converted into charcoal which is valued by silversmiths. The trunks of the trees are used as timber and as water pipes and drains; the terminal bud is eaten as a salad; the fiber of the flower- and leaf-stalks is used in making a kind of rope; the leaves are used for fuel, roofing, and fencing; the

[1] *Malayan Agricultural Jour.* **10**: 4–12. Jan. 1922.

[2] The generic name *Phoenix* refers to Phoenicia, indicating that this palm was cultivated by the Phoenicians. The specific name means "bearer of dactyli" (Latin plural for fingers, alluding to the shape of the fruit). The common name "date" also has the latter derivation.

midribs of the leaves are used in making furniture, bird-cages, and other articles; the leaf-bases are used by fishermen for floats; and the baskets in which dates are packed for shipment are made

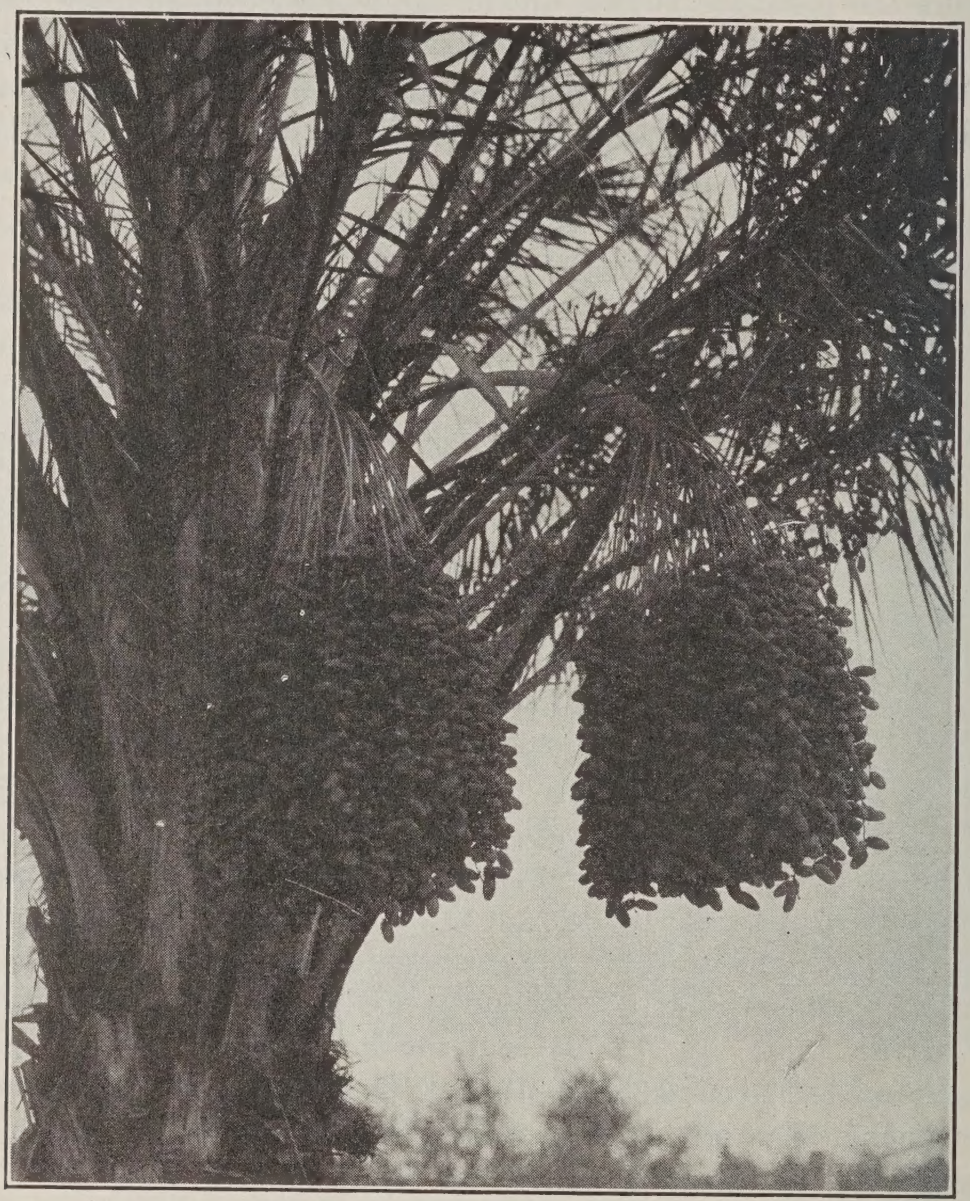


FIG. 611.—Portion of a Date Palm (*Phoenix dactylifera*) bearing two clusters of dates, grown at Secation, Arizona, in 1921. (After King, U. S. Dept. Agr. Dept. Cir. 277.)

entirely of the leaflets. In the oases of the Libyan desert dates have served as money for the payment of fines and tribute. Dowson estimates that the number of uses of the date palm and of the articles made from its products is in the neighborhood of

eight hundred. The average yield of the date crop is used as a basis of taxation in Mesopotamia. A date market in Algeria is illustrated in Fig. 612.

There is evidence that the date has been in cultivation for at least 5000 years. Its original habitat is unknown. The most important date region in the world is probably the country bordering the river Shat Al'Arab, which is formed by the confluence of the Tigris and Euphrates Rivers at Qurna and empties into the Persian Gulf at Fao. The region between these two cities, a distance of 108 miles, is lined with date gardens on both sides

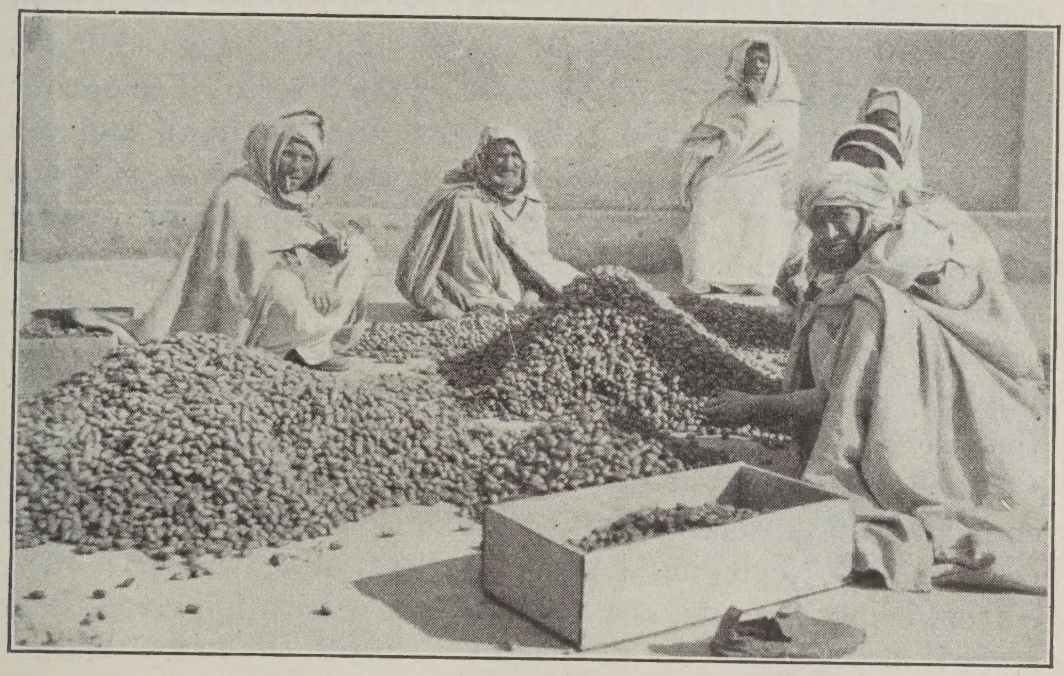


FIG. 612.—Date merchants in the Sahara in Algeria. (After Popenoe, West India Gardens, Altadena, California.)

of the river in Persia and the province of 'Iraq, Mesopotamia. Dowson states[1] that this belt, averaging one mile wide, comprises about 138,000 acres, with 140 palms per acre, or a total number of fifteen to sixteen million. The next largest center of date cultivation in Mesopotamia is Baghdad, farther up the river Euphrates. Nearly every town in 'Iraq is surrounded with date palms. The total number of date palms under cultivation in the world has

[1] Dowson, V. H. W. Dates and date cultivation in the 'Iraq. Agr. Directorate, Ministry of Interior. Memoir III, p. 4–5. Cambridge, Eng., 1921.

been estimated at about 87,000,000, of which, only about 250,000 are grown in America (150,000 in Southern California, and 100,000 in Mexico).[1] To facilitate irrigation the palms are planted in long straight rows.

It is an immemorial custom of the Arabs to take with them, wherever they wander, the seeds of their favorite plants, and in this manner the date was introduced by them into Spain. The large forest of 60,000 palms near Valencia is said to be all descended from one original tree which was planted near Cordova with much ceremony by the first caliph. The date is one of the commonest plants in the oases of the Sahara, because, better than any other plant, it can withstand the very intense heat and bright sunlight, and the severe sand storms of the desert. The olive is the only other tree that can stand these conditions at all, and was the commonest tree of the oases during the occupation of Africa by the Romans. Some of the trees growing at this period are said to be still standing—"giant stems 1500 or 2000 years old."[2] But even the olive grows best under the shade of the date palms, and this shade is indispensable for such other fruit trees as fig, jujube, pomegranate, almond, peach, orange, and others. Under the shade of these other trees garden vegetables are often grown. Of such "subsidiary crops" grown in date gardens, Dowson enumerates 25 species of fruit trees and some 44 species of herbaceous plants, including beets, cucurbits, rice, wheat, barley, cotton, hemp, peanuts, and others. The cultivation given these crops is also sufficient for the palms. Thus the botanical characteristics of the date-palm make possible three different crops. These characteristics are the need of abundant water at the roots, and ability to withstand hot, dry air, and intense winds, provided the water requirements of the roots are met. Proper irrigation requires 110–180 gallons per tree a day, part of which is lost by evaporation and part by seepage.

Since the transportation of dates is also the chief work of the great caravans of camels, we may begin to realize in some measure

[1] Popenoe, Paul. The distribution of the date palm. Geog. Rev. **16**: 117–121, Jan. 1926.

[2] Swingle, Walter T. The date palm and its culture. Year Book U. S. Dept. Agr. for 1900. pp. 453–490. I have freely drawn on this article and on Dowson's memoir for some of the data given above.

the economic importance of this palm; it is the very foundation of desert agriculture and commerce.

As the date requires such a bountiful supply of water at its roots, but cannot set fruit well under conditions of abundant rain, especially during the fruiting season, it thrives best in a region where the water has to be supplied by irrigation. It is interesting to note that this palm not only enjoys warm air but warm water at its roots. In northern Africa the irrigating water in summer commonly has a temperature of 75°–77° F., while in some cases water is used from hot springs, with a temperature as high as 95° F. The date can withstand either fresh or salt water, the water always being salt at and near Fao during spring tides.

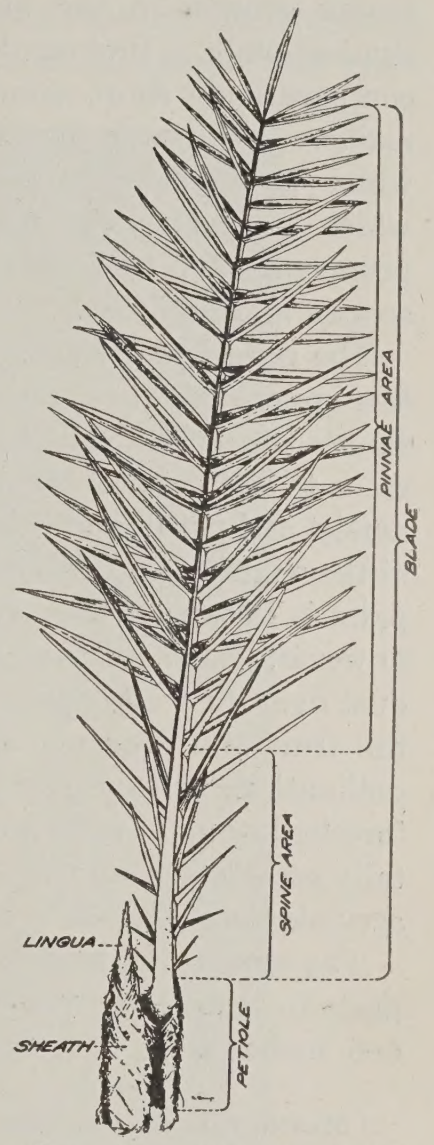


FIG. 613.—*Phoenix dactylifera*. Typical leaf. (After Mason. U. S. Dept. Agr. Bull. 223.)

In contrast to the many-branched trees of the temperate zones, the date (like most palms) is normally unbranched, having only one bud which is at the apex of the trunk. This palm, however, produces numerous suckers near the base of the stem, and is propagated vegetatively by means of these.

The pinnately compound leaves attain a length of 10–15 feet, and 12–20 leaves are formed in a year. They may remain green and physiologically active for a number of years. In the date-growing countries of the old world the natives distinguish the different varieties by the habit of the tree and by the leaf characters, and the United States Department of Agriculture has published a Bulletin on the botanical character of the leaves, in order to make possible a precise and systematic comparison and tabulation of leaf characters, as an aid in determining different

varieties before they come into flower.[1] It will not be desirable to go into these details here. The outstanding characters of what may be called a "typical" leaf are shown in figure 613. At the leaf-base is a sheath of brown fibers which encircles the young growth in the bud. The side of the sheath opposite the leaf-stalk is prolonged into a pointed togue or *lingua*. The comparatively short *petiole* is continued through the *blade* as a *rachis*. The lower part of the blade proper consists of spines which gradually give place to true photosynthesizing pinnae which extend to the tip of the leaf. The arrangement and proportions of these parts are characteristic for the different species and varieties.

The date is dioecious. This was recognized, though more or less imperfectly, by Theophrastus,[2] who says, in his *Enquiry into Plants* (Bk II, § VIII, ¶4): "With dates it is helpful to bring the male to the female; for it is the male which causes the fruit to persist and ripen, and this process some call, by analogy, 'the use of the wild fruit.' The process is thus peformed: When the male palm is in flower, they at once cut off the spathe on which the flower is, just as it is, and shake the bloom with the flower and the dust over the fruit of the female, and, if this is done to it, it retains the fruit and does not shed it." This description of artificial pollination, written over 2000 years ago (see, also, p. 873), is the foreshadowing of our knowledge of sex in plants, first experimentally established by Camerarius and published in his treatise, *De sexu plantarum*, 1694.

The very small white staminate flowers have a perianth with parts in threes, and six stamens. A branch of the inflorescence 4–6 inches long may bear 20–50 flowers or 120–300 stamens

[1] Mason, Silas C. Botanical characters of the leaves of the date palm used in distinguishing cultivated varieties. U. S. Dept. Agr. Bul. 223. Washington, D. C., June, 1915.

[2] THEOPHRASTUS, pupil of Plato and of Aristotle (also the author of books on plants), was born at Eresos, in Lesbos, 370 B.C. Aristotle, in his will, left his garden in the grounds of the Lyceum (Athens) to Theophrastus. Here we have the ancient analogy of what we should, in modern terms, describe as the first director of the first botanic garden of which we have definite record. The observations recorded in the botanical writings of Theophrastus were based in part on his observations of the plants in this garden. He died about 285 B. C.

(Fig. 614). The pistillate inflorescence (like the staminate) is enclosed in a sheath when young. By the growth of the inflorescence the sheath is forced open, and at this stage pollination may be accomplished.

In nature, staminate and pistillate plants are produced in about equal numbers, and when the trees grow in this proportion wind-

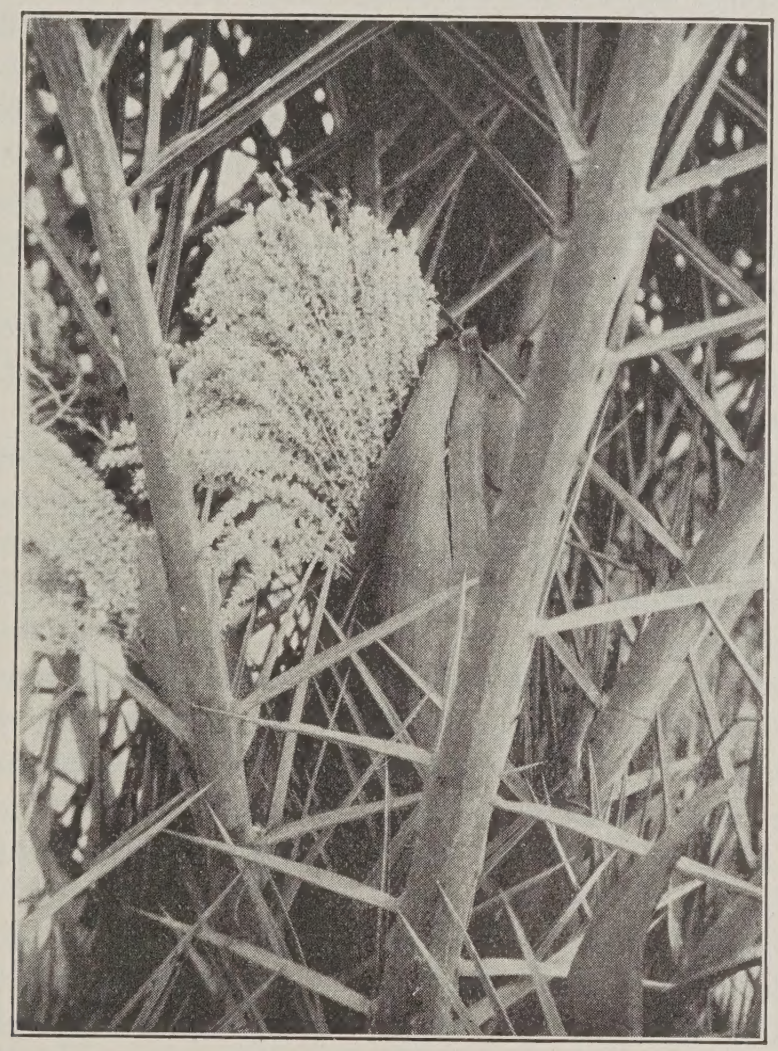


FIG. 614.—*Phoenix dactylifera.* Staminate palm in flower at Tucson, Arizona. on September 11, 1924. (Photo by Frank Stoll.)

pollination is sufficient. It is not economical, however, to allow so many staminate palms in a date orchard. The ancient Assyrians discovered this some 3000–4000 years ago, and adopted the practice of growing only one staminate palm to about 50 or 100 pistillate ones. This greatly reduces the chance of wind pollina-

tion and the ovaries of unpollinated flowers develop into small, stoneless fruits, of little or no value. Therefore, to make sure of a high percentage of pollination a man (*fellah*) takes a portion of the ripe staminate inflorescence and inserts it firmly in the middle of each pistillate inflorescence. When pollen happens to be scarce, or where a large number of pistillate inflorescences are to be pollinated in a short time, the pollen is shaken out and tied up in a bag of fine muslin, fastened to the end of a stick. With this the fellah dusts the pistillate inflorescences.

It is not important that all the stigmas become receptive at the time the pollen matures, for the date pollen will remain viable for from several weeks to two years or more. This is one of the longest periods of pollen viability known (*Cf.*, also, p. 367).

In certain places in Mesopotamia land is so valuable that no staminate palms at all are grown, the pollen being imported from Fao, at the mouth of the Shat Al'Arab, where the salt water is not so favorable to the growth of palms.

Wind-pollination has been known to take place when the staminate tree was from one half a mile to a mile from the pistillate trees, but the result is uncertain and many stigmas fail of pollination, so that this method cannot be relied upon for successful crops.

The date is more resistant than any other palm to extremes of temperature, being able to survive a range of 4°–125° F. The geographical range where it may be grown is, however, much wider than the range where it produces fruit successfully, some varieties being more exacting than others in their temperature requirements.

According to Mason,[1] this is believed to be due largely to structural peculiarities. The active growing tissue is confined to the large terminal bud, called the *phyllophore* because it produces the leaves. Here the growth of the trunk in diameter and length, and the basipetal growth of the leaves and flower spathes are in progress simultaneously. With favorable temperature and water supply growth is continuous throughout the year.

Thermometers inserted in the growing tissues of the bud show a remarkably uniform temperature, not fluctuating greatly, if at all, with changes in atmospheric temperature, but corresponding

[1] Mason, Silas C. Jour. Agr. Res. **31**: 401–468. Sept. 1, 1925.

closely with the soil temperature surrounding the roots. This uniformity is explained by Mason as due chiefly to two factors, as follows:

"1. *A protective envelope surrounding the growth center*, of a highly nonconducting and insulating nature, composed of the thick, fibrous, overlapping leaf bases, with the accompanying fibrous sheath and lower down the outer zone of the trunk proper. Through these layers the air temperatures, cold or hot, penetrate very slowly and with considerable loss.

"2. *The ascending sap current*, with a temperature acquired from the soil from which it is drawn by the roots. Under the insulation afforded by the protective layer and the outer portions of the trunk, the sap is able to reach the growth center at a temperature varying but a few degrees from that at which it left the soil, and so is able to neutralize much of either cold or heat, as the case may be, that has penetrated from without.

"It is believed that in the discovery of this stabilizing of the temperature of the growth center of the date palm is disclosed a principle heretofore unrecognized in plant physiology, and one of vital importance to palms and other endogenous plants in desert environments in enabling them to survive the extremes of their temperature exposures."

Leaves of the date palm grow in groups of three to five, each group being called a *palus*. This growth takes place at the base, and elongation ceases in all tissues as soon as they are exposed to the full sunlight, owing to the inhibiting effect of the yellow, violet, and (probably) the ultra-violet rays. Growth of the protected tissues occurs chiefly between sunset and sunrise, and at a reduced rate during the day. The tissues are so sensitive to light that growth may be induced by merely screening the plant from direct sunlight, leaving it exposed only to the reflected light from the north side. According to Mason, growth in the dark is correlated with the closing of the stomata, which takes place in reduced light or darkness, with a resultant reduction in transpiration.

On the delta of the Nile today it is customary to plant one staminate to about 20 pistillate palms; Toumey recommends a ratio of about one to six or eight around dwellings in Arizona.[1]

[1] Toumey, J. W. *The date palm.* Univ. of Arizona. Arizona Agr. Exp. Sta. Bul. 29. Tucson, 1898.

The date-palm flowers from April to June (depending upon location and other conditions). There are three carpels to each pistillate flower, but only one of them matures, even though pollinated. The other two drop off. In maturing, the fruit

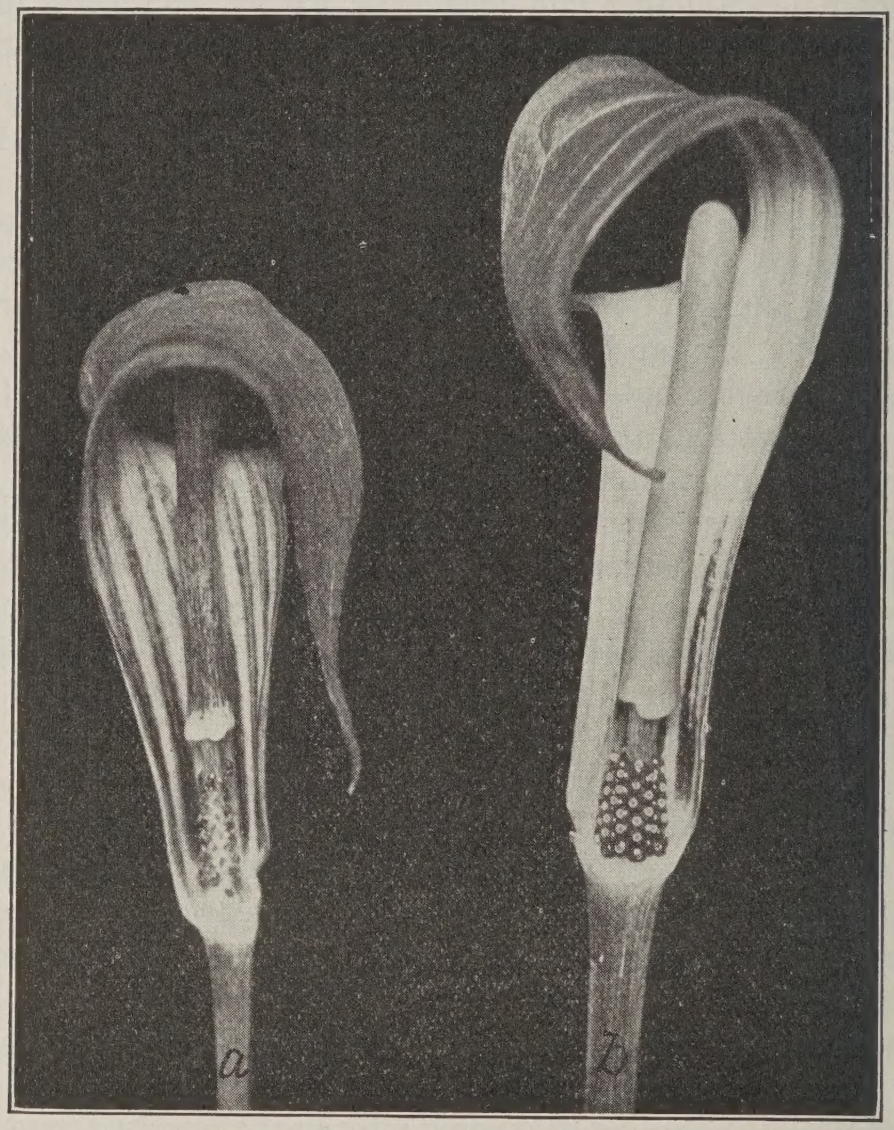


FIG. 615.—Jack-in-the-Pulpit (*Arisaema triphyllum*). The spathe has been cut away so as to disclose the spadix with flowers at the base. *a*, staminate, *b*, pistillate flowers. More frequently this plant is monoecious. (Photo by E. M. Kittredge.)

changes from white to green, then to bright red or yellow, when ripening begins. In ripening, the fruit becomes amber, reddish brown, or black, changes of texture occur, the astringency of the green fruit, due to the presence of tannin, disappears, giving place to sugar which may form 60% of the dry weight of ripe

dates. The amount of sugar varies with the variety. Dowson states that the choicest fruit is not sold, but is eaten by the garden owner.

It may be added here that ancient tablets from Umma and Nippur show that large date orchards existed in the Tigris-

FIG. 616.—Water Arum (*Calla palustris*). The upper flowers on the spadix tend to be staminate; the others perfect. (Photo by E. M. Kittredge.)

Euphrates delta as early as 2400 B.C., that artificial pollination was practiced then, and that staminate trees were grown apart from the pistillate.[1]

[1] Scheil, V. De l'exploitation de dattiers dans l'ancienne Babylonie *Revue d'Assyriologie*, 1913. See, also, p. 868.

The cultivation of dates in the United States from seeds was attempted by the Mission Fathers in the eighteenth and early nineteenth centuries, and again by early American pioneers from 1848 to 1880, but without success, as so large a proportion of the seedlings were staminate, and the pistillate trees proved to be of an inferior quality. Suckers were imported in

FIG. 617.—Ceriman (*Monstera deliciosa*). Leaves and ripening fruits. The fruits are about twice the size of a large banana. Cf. Fig. 230.

1876–1880, but the success of American date culture began with the importation of suckers of choice varieties from the Sahara in 1899–1901. This was done by the U. S. Department of Agriculture in cooperation with the University of Arizona and the Arizona Agricultural Experiment Station. Successful plantations have been established in California (San Joaquin and

Sacramento River valleys, and the Colorado Desert region), in Arizona, and other parts of the southwestern United States.[1]

ORDER, Arales

The Arales are succulent herbs with the inflorescence a fleshy spadix, enclosed with or suspended by a spathe; in some forms the spadix is naked. Here belongs the Arum Family (Araceae), represented in the United States by the well-known Jack-in-the-Pulpit (*Arisaema triphyllum*) (Fig. 615), the Arrow-arum (*Peltandra*), Water Arum (*Calla palustris*) (Fig. 616), Skunk Cabbage (*Symplocarpus foetidus*), Golden Club (*Orontium*), and Sweet Flag or Calamus Root (*Acorus Calamus*).

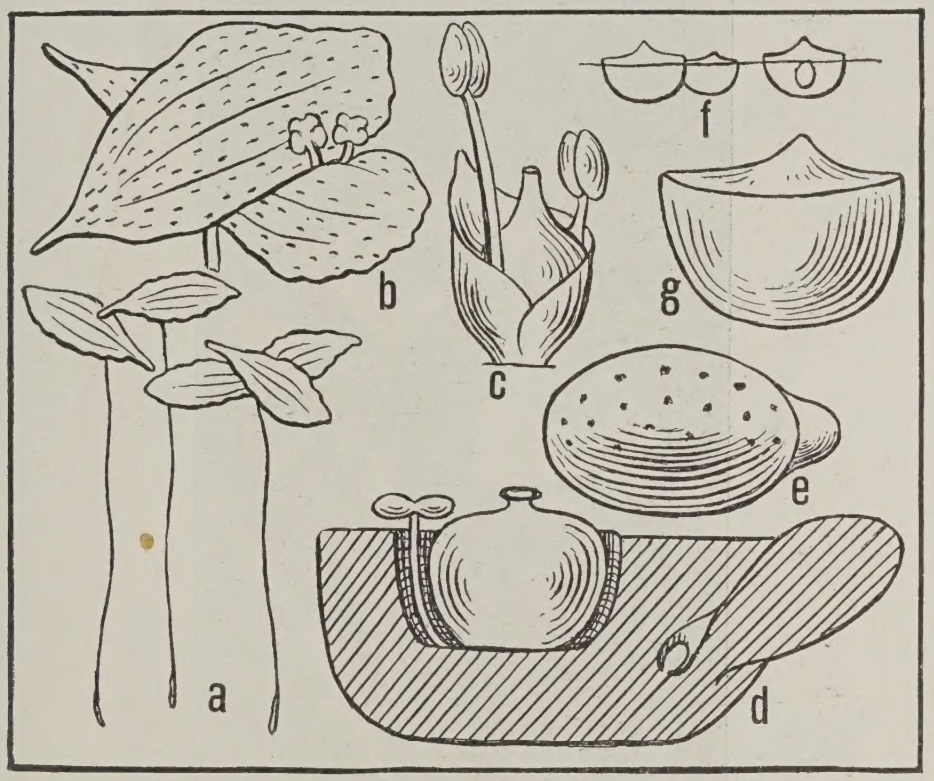


FIG. 618.—*a, b, c, Lemna trisulca; d, e, Wolffia punctata; f, g, Wolffia papulifera.* (Redrawn from Britton and Brown, slightly modified.)

Among sub-tropical and tropical Araceae are the cultivated Calla Lily (*Richardia*), the Tail-flowers (*Anthurium*) of our

[1] Toumey, J. W. The date palm. Arizona Agr. Exp. Sta. Bull. 29. June, 1898. Professor Toumey was a pioneer in the matter of the successful introduction of date culture in the United States, and his bulletin has been called "the most important study of the date palm ever published in America."

northern conservatories, and the *Caladium* (a foliage plant). The Yautias (yow-tee′-ah), species of *Xanthosoma*, of the West Indies, and the Taros (tah′ ro), species of *Colocasia*, common throughout the tropics and sub-tropics, are cultivated for their starchy edible rhizomes, which in many parts of the tropics hold a place similar to the potato in temperate regions. The

FIG. 619.—Spiderwort (*Tradescantia virginiana*). (Photo by E. M. Kittredge.)

Egyptian taro is *Colocasia antiquorum;* those from the islands of the Pacific and southern Asia are apparently varieties of *C. esculenta*, including the common "Elephant ear" (often called *Caladium esculentum*). The most important varieties of *C. esculenta*, the Dasheens, came to the United States from Trinidad. The name (dasheen, da Chine, *de la Chine*) implies that it came originally from China. One of the most interesting of the Aroids

is the Ceriman or "Delicious Monster" (*Monstera deliciosa*), commonly grown in northern greenhouses. It is found in the American tropics growing as a climber or trailer, and is said to fruit better when trailing on the ground. The large leaves have numerous perforations and marginal incisions, and this is said to be an advantage to the plant by allowing more sunlight to reach the lower leaves, which would otherwise be excessively

FIG. 620.—Pickerel-weed (*Pontederia cordata*). (Photo by E. M. Kittredge.)

shaded by the large leaves above. The plant bears numerous aerial roots. The flower (Fig. 230) resembles a large calla-lily, and the "fruits" (ripened spadix, Fig. 617), have a flavor suggesting, at the same time, the banana and the pineapple. They are edible only when thoroughly ripe, as they are full of *raphides* (acicular crystals) when unripe.

The Arales include, also, the highly modified aquatic spermatophytes, the Duckweeds, Lemna, Wolffia (Fig. 618), and some

thirty or more other species, included by some authors in a separate family, the *Lemnaceae*. These all illustrate regressive evolution, that is, reduction from more highly developed ancestors. They include the simplest and, some of them, the smallest of all seed-bearing plants. The plant body has been variously

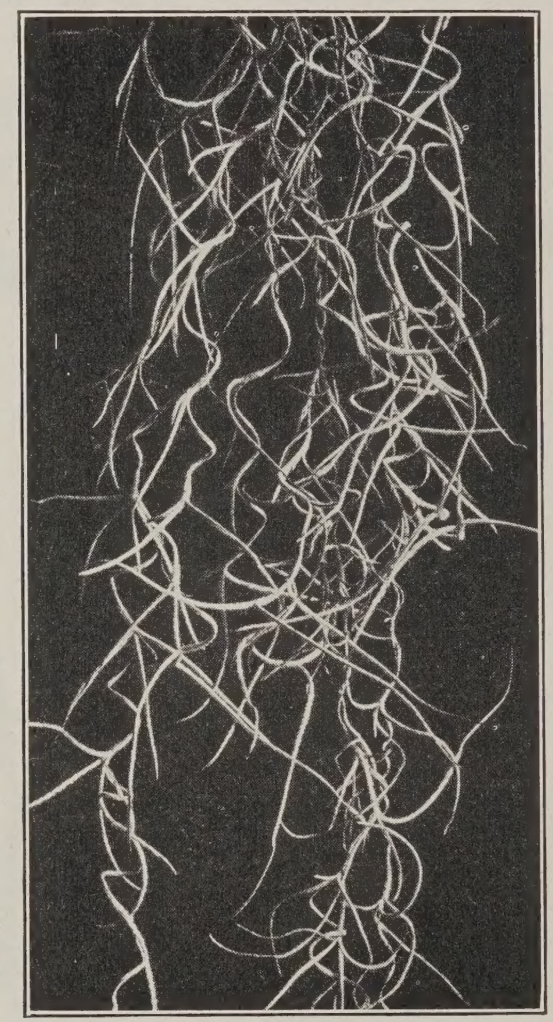


FIG. 621.—Florida "moss" (*Tillandsia usneoides*).

interpreted as a frond and a leafless stem. Goebel considers it a *free-living leaf*, since the first structure produced by the germinating seed is only a matured cotyledon.

ORDER, **Xyridales**

The *Xyridales* comprise, among other families, the Yellow-eyed-Grass Family (*Xyridaceae*), the Pipewort Family (*Erio-*

caulaceae), the Spiderwort Family (*Commelinaceae*), including the spiderwort (*Tradescantia*) (Fig. 619) and the Day-flower (*Commelina*), a rather common weed in dooryards in the northeastern United States; the Pickerel-weed Family (*Pontederiaceae*) represented east of the Mississippi River from Nova Scotia to Texas by the aquatic Pickerel-weed (*Pontederia cordata*) (Fig. 620), and the Mud-plantain (*Heteranthera*).

FIG. 622.—Pineapples (*Ananas sativus*), growing in Florida.

One of the economically important families of the Xyridales is the Pineapple Family (*Bromeliaceae*). Here belong forms so unlike in general appearance and habit of growth as the so-called Florida "moss" (*Tillandsia usneoides*, Fig. 621) and the edible Pineapple (*Ananas sativus*), both native American plants.

The "pineapple" of commerce Fig. 622) is a fleshy multiple fruit, technically called a *sorosis* (sisterhood). The floral axis is terminal on the plant, and above the region of the flowers it

develops into a short leafy stem; when this is cut off it may be rooted as a cutting. This is the customary method of propagating pineapples. The inflorescence is a spike, similar, in this respect, to the plantain (*Plantago*) or Mullein (*Verbascum*). The floral organs, bracts, and axis all blend, in ripening, to form the fleshy, juicy "pineapple." The fruit itself (botanically speaking) is a seedless berry (Fig. 623).

FIG. 623.—Pineapple (*Ananas sativus*). (From LaMaout and Decaisne.)

ORDER, Liliales

The order Liliales is characterized by flowers having, as a rule, three carpels which are united to form a compound pistil. The parts of the perianth are in two whorls of three each, the sepals resembling the petals, and all inserted below or above the pistil (*i.e.*, ovary superior or inferior). There are about 10 or 15 families, the number varying according to author.

LILY FAMILY

The *Lily Family* (*Liliaceae*) comprises nearly 200 genera and some 2000 or more species, including herbs and, in rare cases, woody plants, a large proportion of which are in cultivation. The six stamens are inserted each opposite a perianth-lobe, and the fruit is a few to many-seeded pod or berry. The seeds have endosperm. By some authors the family is subdivided into more than a dozen tribes, while other authors organize the same groups

FIG. 624.—Umbel of onion (*Allium Cepa*).

into various separate families. Among the genera of horticultural or agricultural importance are the following:

The onions (*Allium*), containing nearly 300 species widely distributed—some 50 or more being found in the United States. All the species bear bulbs and possess the characteristic odor of the common garden onion. The bulbs are either clustered or solitary. *Allium* leaves are usually cylindrical and hollow, and the flower-cluster is a rather spherical umbel (Fig. 624). The wild

plants include the Wild Leek (*Allium tricoccum*), Wild Garlic (*A. canadense*), Field Garlic (*A. vinelae*), Wild Onion (*A. cernuum*), and others. The most familiar and important, of course, are the English Garlic (*A. sativum*), Shallots (*A. ascalonicum*), Chives (*A. Schoenoprasum*), and the common Garden Onion (*Allium Cepa*). The word *allium* was the ancient Latin name for garlic; the word *Cepa* (*coepa*) was Pliny's translation of the Greek word used by Theophrastus for an onion—hence the binomial, *Allium Cepa*, meaning literally, onion-garlic. This is among the very

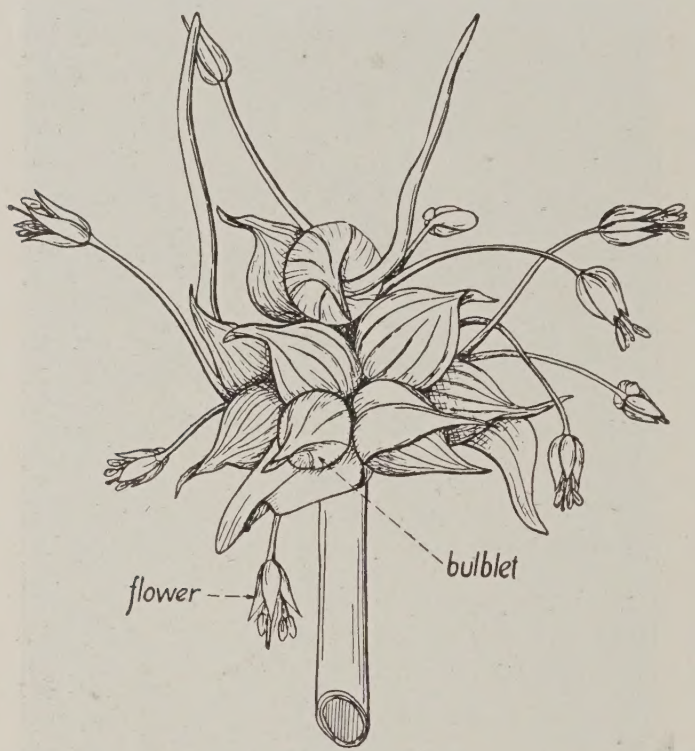


FIG. 625.—Top onions. Cluster of bulblets which have replaced the inflorescence. (After Robbins.)

earliest of cultivated plants, being well known to the ancient Egyptians, Hebrews, Greeks, Romans, Chinese, Hindoos, and others.

Onions are propagated by seeds and by "sets" (small bulbs and bulbils). In "multiplier onions" (*Allium Cepa* var. *multiplicans* Bailey), the bulb contains two or more hearts instead of one, and when planted this compound bulb separates into its parts, each one sending up leaves and forming an "onion."

In the "top-onion" (*A. Cepa* var. *bulbellifera* Bailey) bulblets are formed at the summit of the flower stalk, in the place of flowers,

and sometimes associated with flowers (Fig. 625). The bulblets may be used as sets.

The genus *Hemerocallis*, with about 5 species, is a native of Europe and Asia, and has become established in North America as an escape from cultivation, in meadows and along streams. The Day Lilies (*Hemerocallis fulva*, and *H. flava*) do not, ordinarily, set seed.

The genus *Lilium* (Lily), from which the family derives its name, comprises over 60 species, at least 35–40 of which are in

FIG. 626.—Wood lily (*Lilium philadelphicum*).

cultivation. The genus has been divided by Waugh[1] into six sub-genera. Among the better known cultivated lilies are the Easter Lily (*L. longiflorum* Thunberg var. *eximium* Nichols = *L. Harrisii* Carriere), *L. Japonicum* Thunb., Madonna Lily (*L. candidum*), *L. bulbiferum* and the Tiger Lily (*L. Tigrinum*) (both bearing black bulbils in the axils of their leaves), *L. elegans*, European Turk's Cap Lily (*L. Martagon*), more cultivated in Europe than in America, and many others. Among wild North American

[1] Waugh, F. A. A conspectus of the genus Lilium. Bot. Gaz. **27**: 235–254, 340–357. 1899.

species, many of which are also cultivated in gardens, are *L. philadelphicum* (Fig. 626) and the American Turk's Cap Lily (*L. superbum*).

THE TULIP

The genus *Tulipa* derives its name from the Persian word *toliban*, from the fancied resemblance of the inverted flower to a turban. It was introduced into Europe from Turkey about 1554, but Turkish manuscripts of the 14th century mention several varieties. Conrad Gesner first saw the plant growing at Augsburg, Germany, in 1559; about 1577 it was introduced into England, possibly by Clusius (1525–1609), the famous Dutch herbalist. It was not Clusius who introduced the plant into Holland, but by 1591 he was raising tulips for sale at high prices in Holland, and his plants stimulated the interest in tulips which culminated in the famous tulip-mania in Holland, which continued from 1634 to about 1638. People speculated in tulip bulbs as now in stocks, and often no bulbs changed hands. As much as 13,000 florins was paid for a bulb of the variety "Semper Augustus." Finally the Dutch government intervened and passed laws to end the wild speculation.

Classification.—Gesner designated the plant as *Tulipa Turcarum* (Tulip of the Turks), and Linnaeus (in 1753) referred all the tulips with which he was acquainted to *Tulipa Gesneriana*. About 1797 a fragrant, early blooming, wild tulip was discovered in southern Europe and named, by Roth, *Tulipa suavolens*. This is thought to have been an escape from gardens, and not a native wild plant. It is the source of the Duc van Thol group and other early flowering varieties. The late flowering sorts are probably derived from the so-called *T. Gesneriana*. All of this early history, however, is more or less uncertain.

Color of Petals.—1. With the exception of a few pure white or yellow varieties, there is a blotch of color at the base of each petal next the ovary. This varies from blue or black to white or yellow, depending on the group and variety. This blotch is not included when speaking of the color of the flowers.

2. In addition to the basal blotch, the petals of all tulips contain a yellow or white pigment dissolved in the cell-sap of the mesophyll cells. In white and yellow "selfs" this is the only pigment present.

3. In many other forms there is also present an anthocyanin pigment in the epidermis. This varies from red to purple and rose. By peeling off the epidermis this color is, of course, removed, leaving the petals white or yellow. When the colored epidermis overlays white mesophyll tissue the epidermis determines the color of the flower; if it overlays yellow mesophyll, we have the various shades of brown, orange, and scarlet, and the "bizarre" forms.

4. Some tulips also have another, yellowish, pigment present in the epidermis with the reddish anthocyanin, giving a flushed effect.

Breeder Tulips.—When tulips containing anthocyanin pigment are raised from seed, the first flower of the seedling is always of uniform color (except, of course, for the base of the petals) and is called by the gardeners a "self-colored" flower or "self." These plants are also called "breeders" because after one or more seasons the offsets will "break" and produce flowers not of uniform color, but having the epidermal color confined to the edges or the center of the petals; the shade may also become darker, the leaves may be mottled, the stem may have anthocyanin pigment, the vigor and size of the plant may be diminished, and the bulbs may not throw as many offsets. The cause of breaking is not known, but all garden tulips (except the "selfed" yellows and whites) may break, and a "broken" bulb never returns to a breeder nor gives breeder offsets. There is no way known either to cause or to prevent breaking. This makes it difficult, if not impossible, to classify tulips according to color.

Tulip Droppers.—When tulip bulbs are not planted at a level suited to their best development they produce at the base a peculiar structure known as a "dropper" or "sinker." These droppers are hollow cylinders, part stem and part leaf. When the lower end of the dropper has reached the suitable level in the soil a new bulb develops there. In cases where the old bulb was too deep the dropper will turn and grow upward to the suitable level and then form the new bulb. Droppers have also been observed in the Dog's-tooth-violet (*Erythronium*), but in most species of bulbous plants the bulbs burrow by means of contractile roots (*Cf.* p. 107).

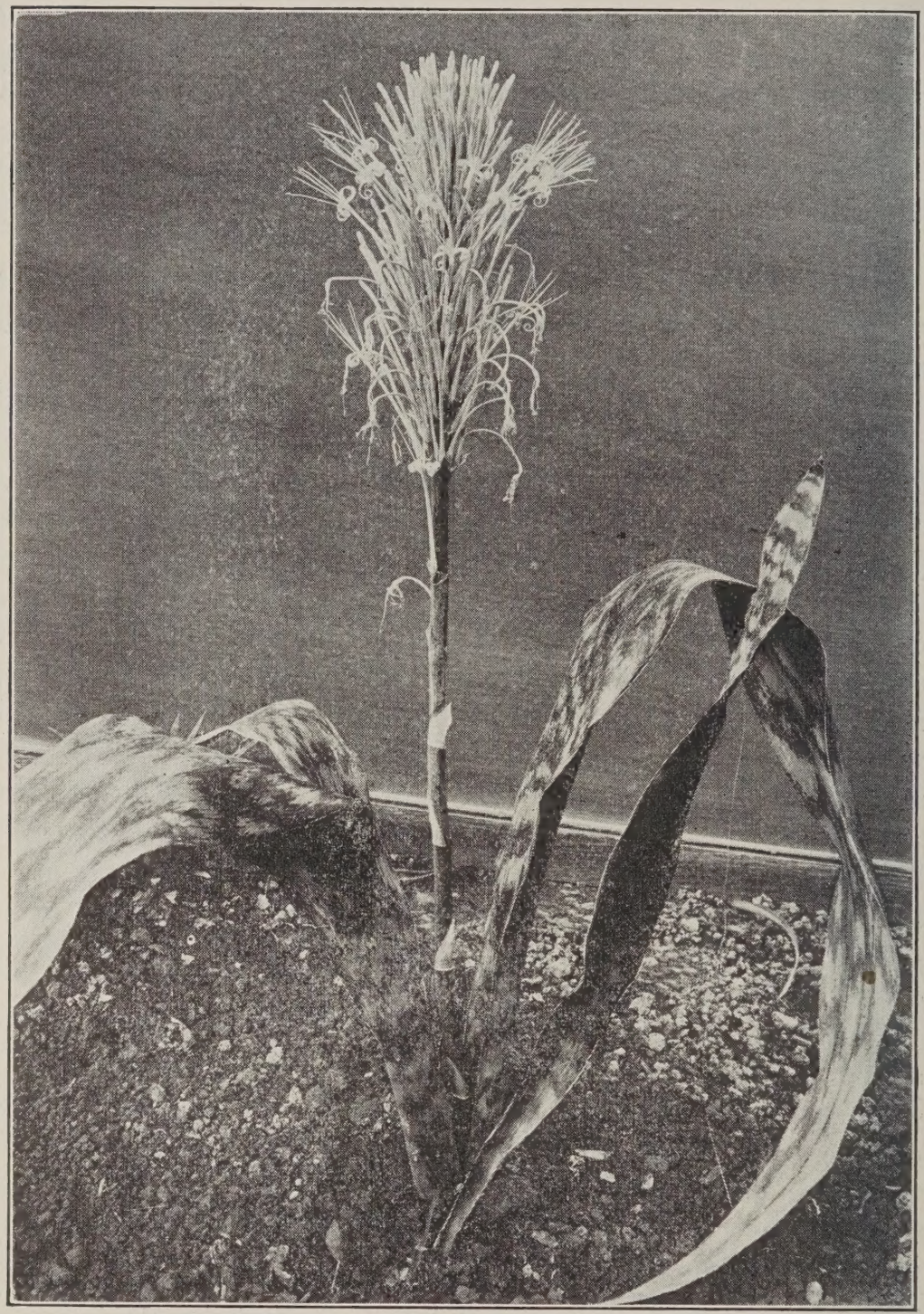


FIG. 627.—African Bowstring-Hemp (*Sanseviera guineensis*).

OTHER LILIACEAE

The Lily Family also contains the following genera, more or less well known in either wild or cultivated forms: *Fritillaria*, with adout 50 species, the best known of which in cultivatiob is the Crown Imperial (*F. imperialis*); Guinea-hen Flower (*F. meleagris*), *Erythronium* (Yellow Adder's Tongue, Dog's-tooth-violet, Fawn Lily); *Calochortus* (Mariposa Lily); *Camassia* (Wiln

FIG. 628.—Flowering plant of *Yucca filamentosa*.

Hyacinth); *Ornithogalum* (Star-of-Bethlehem); *Muscari* (Grape-Hyacinth), adventive from southern Europe and escaped from gardens. The blue flowers of *Muscari*, bunched like grapes, sometimes have a distinct odor of musk, whence the generic name. In the Lily Family also belong the Colic-root (*Aletris*); the Spanish Bayonet (*Yucca*), with some 16 species; the *Dracaena*, common with the florists; *Aloe; Phormium tenax* (New Zealand

Flax); and species of *Sanseviera* (earlier spelling *Sansevieria*), the Bowstring-hemp (Fig. 627).

The Yucca (Fig. 628) presents a unique case of insect-pollination, for the Yuccas can be pollinated only by species of the Yucca moth (*Pronuba yuccasella*), and the moth in turn cannot complete its life cycle except in the flowers of the Yucca. The plant and the insect are absolutely interdependent. The facts have been worked out in great detail by Riley[1] and Trelease.

FIG. 629.—Flower of *Yucca filamentosa* with the perianth segments artificially opened out so as to disclose (on the left) an adult female of the Yucca moth (*Pronuba yuccasella*). Note her black eye and black legs. At the right are shown the stamens and pistil before the anthers have shed their pollen and withered.

The female moth (Fig. 629), working always at night, goes from one stamen to another and, with her two maxillary palps, the first joints of which are transformed into long prehensile organs, she collects pollen from several anthers. She then inserts her ovipositor into the soft tissue of the ovary of the flower and deposits her eggs among the numerous ovules. The eggs being deposited, she carries the pollen she has collected to the top of the pistil and forces it into the canal which extends through the length of the style. The stigmatic surface is confined to the

[1] Riley, C. V. The Yucca moth and Yucca pollination. Missouri Bot. Gard. Third Ann. Rept. 1892, p. 99–158. Plates 34–54.

lining of this canal, so that pollination is not effective unless the pollen is deposited in the canal, and Riley states that artificial pollination of Yucca can be accomplished only with difficulty. Accounts of different authors vary as to whether the pollen is collected before or after oviposition.

The larvae now develop along with the seeds, and as soon as the larvae are large enough to eat they feed on the young seeds. No other food can be substituted for the seeds, but there are enough seeds so that some are always left to perpetuate the plant.

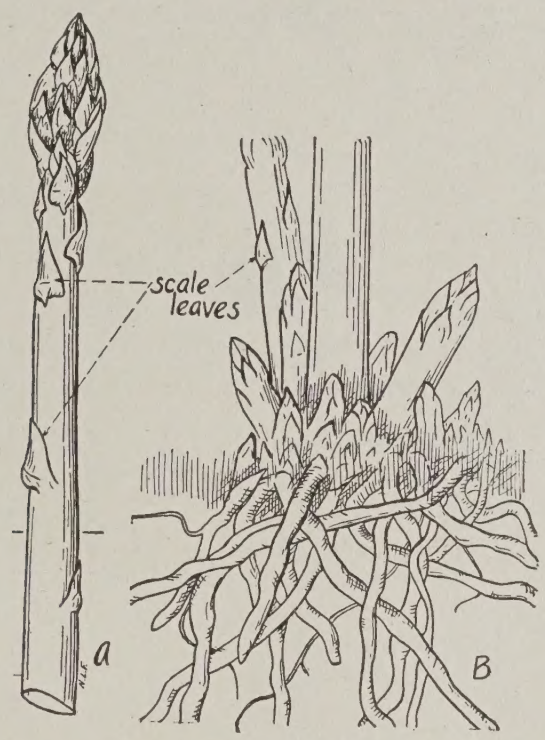


FIG. 630.—Garden asparagus (*Asparagus officinalis*). *A*, young shoot; *B*, roots and young shoots arising from the "crown." (After Robbins.)

When mature, the larvae bore a hole through the seed-capsule and lower themselves to the ground by a slender thread which they spin. They then bore into the ground several inches, and spin a cocoon where they remain until the following spring. About two weeks before the Yuccas begin to flower the insect passes into the pupa state, and emerges just as the flowers are opening. The imago flies up into the corollas and the interesting life-story is repeated.

In the Lily-of-the Valley Sub-Family (sometimes considered a family—Convallariaceae), the most important genus, horticul-

turally, is *Asparagus*. This is an Old World genus containing about 100 species. *Asparagus officinalis* L. is cultivated for the young shoots which are used as a vegetable (Fig. 630). The root is perennial, sending up the tender shoots each spring. The

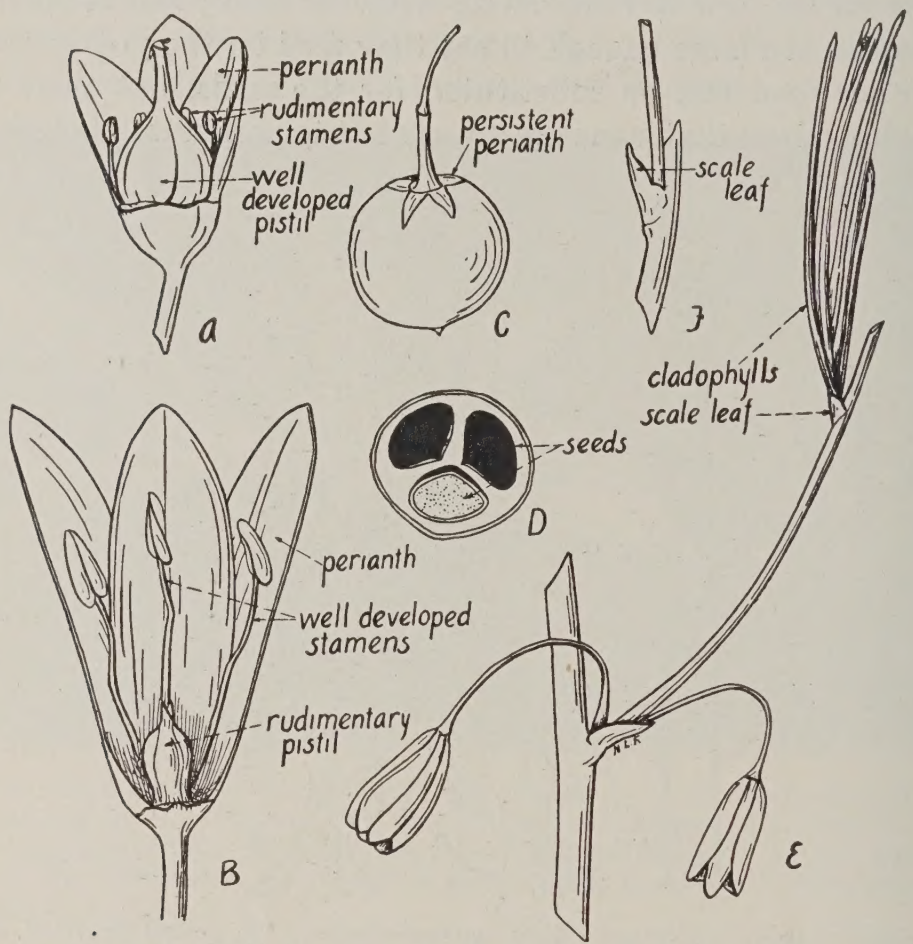


FIG. 631.—Garden asparagus (*Asparagus officinalis*). *A*, pistillate flower; *B*, staminate flower; *C*, mature fruit; *D*, section of fruit; *E* and *F*, portions of the plant showing method of branching, position of flowers and leaves. (After Robbins.)

stems, when allowed to grow, are slender, green, and branched, the numerous finer branches being often mistaken for leaves. The leaf-like appearance of the smaller branches is specially marked in the so-called "smilax" of the florists, *Asparagus medeoloides*.[1] The so-called "asparagus fern" is not a fern,

[1] *Asparagus medeoloides* Thunberg = *Asparagus asparagoides* Wright = *Myrsiphyllum asparagoides* Willdenow. See foot-note p. 893.

but a climbing species of asparagus (*A. plumosus*, or *A. sprengeri*, Fig. 632).

The edible asparagus is dioecious, and the staminate plants yield a larger crop of "spears" than pistillate plants, for most of

FIG. 632.—"Asparagus fern" (*Asparagus plumosus*). Leafy branch bearing flowers and fruit.

the energy and material of the pistillate plants goes into fruit formation. Asparagus is known to have been cultivated for more than 2000 years.

Among the genera of this family found growing wild in North America may be mentioned the *Clintonia*, *Smilacina* (False

Solomon's Seal), *Maianthemum* (May Flower), *Streptopus* (Twisted-stalk), *Polygonatum* (Solomon's Seal), *Medeola* (Indian Cucumber-root), *Trillium* (Wake Robin), and *Convallaria* (Lily-of-the-Valley), the latter also extensively cultivated in gardens and grown by florists.

FIG. 633.—Green Brier (*Smilax rotundifolia*). (Photo by E. M. Kittredge.)

Among other families of the Liliales are the following:

Smilax Family (Smilacaceae), with 3 genera and about 200 species. Only one genus, *Smilax*, occurs in North America, comprising the common Green Brier or Cat-Brier (*S. rotundifolia*, Fig. 633), the Carrion-flower (*S. herbacea*, Fig. 634), and about 175 other species of wide distribution. Many of the species are woody climbers, with the petioles acting as tendrils; others are

shrubs or, more rarely, herbaceous perennials.[1] Some tropical American species of *Smilax* are the source of sarsaparilla.

The *Yam-Family* (Dioscoreaceae) contains some 9 genera and 175 species, mostly American, but a few confined to the Old World. The genus *Dioscorea* has been cultivated in America from prehistoric times. Among the economically interesting species is the *Air Potato* (*Dioscorea bulbifera*), which bears large

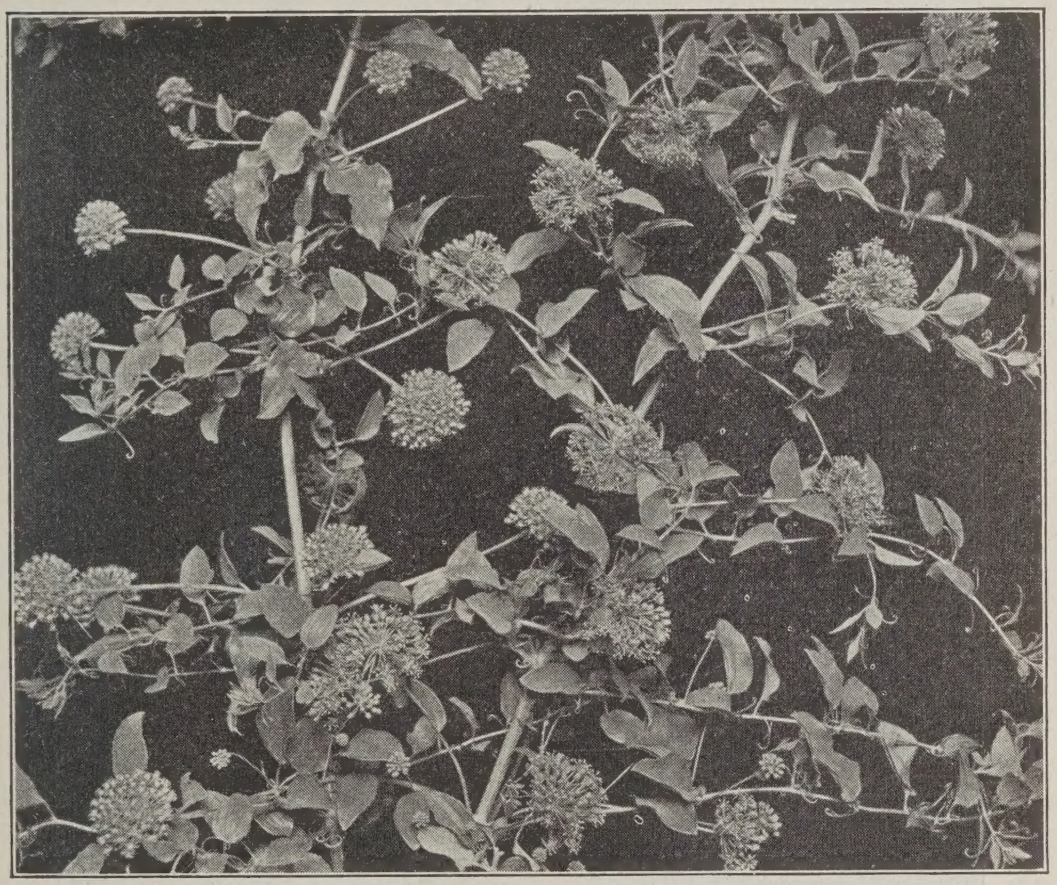


FIG. 634.—Carrion-flower (*Smilax herbacea*). (Photo by E. M. Kittredge.)

edible tubers in the axils of its leaves. The root tubers are usually small or may not develop at all, but the axillary tubers may attain a weight of several pounds. The "greater yam" (*D. alata*), having, as its specific name implies, winged stems, is cultivated in the tropics. Its tuberous root becomes 6–8 feet long, may weigh as much as 100 pounds, and may continue to grow for several years.

[1] The genus *Smilax* is not to be confused with the "smilax" of the florists. *Cf.*, p. 890.

The Chinese Potato or Yam[1] (*Dioscorea divaricata* Blanco = *D. Batatas* Decaisne) is a tall, climbing vine, with cinnamon-scented white flowers in the leaf-axils. The deep-growing root-tubers may attain a length of 2–3 feet (Fig. 635). When the

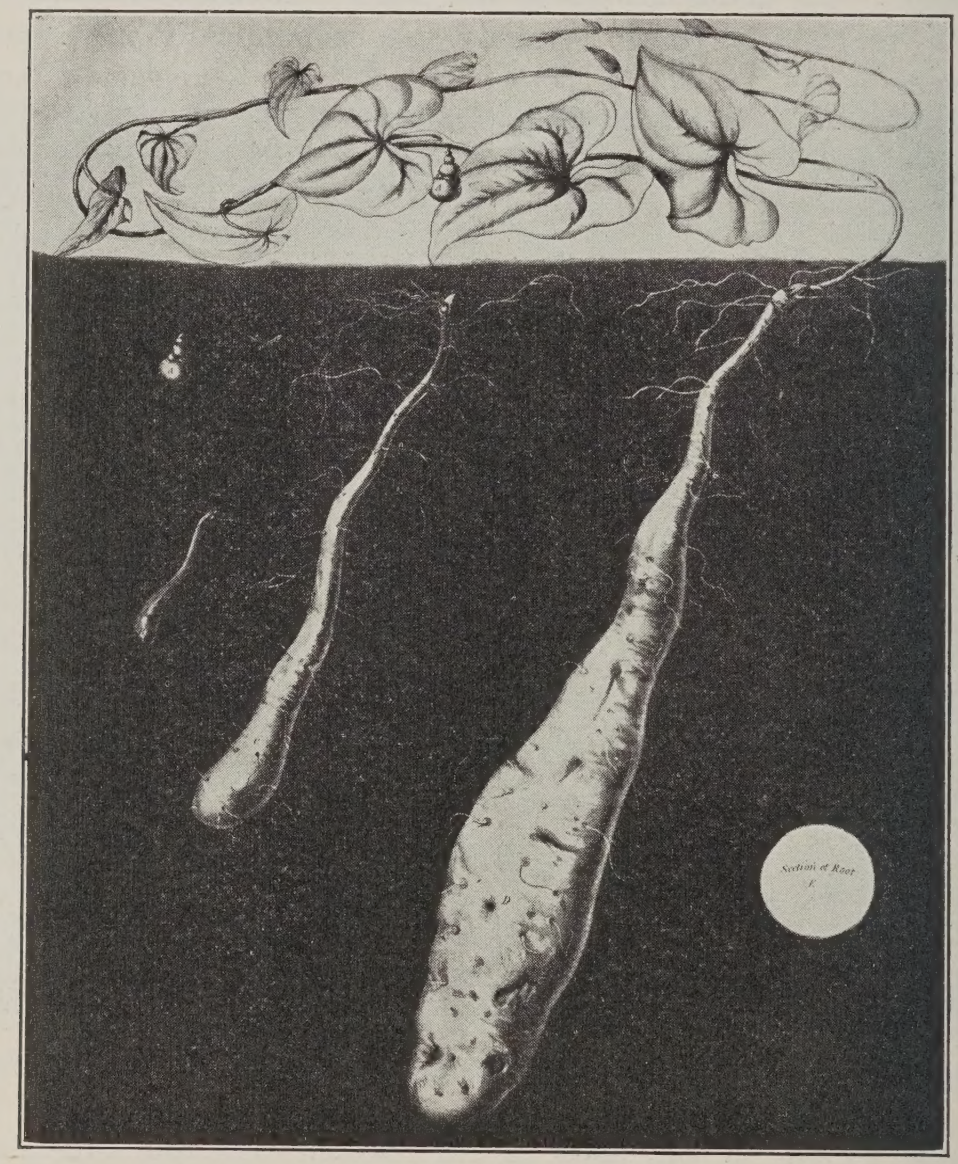


FIG. 635.—Yam, or Chinese Potato (*Dioscorea Batatas*). *A*, Tuber; *B*, *C*, *D*, Roots; *E* about $\frac{1}{6}$ natural size. (Reproduction from a print published by W. R. Prince and Co., Flushing, N. Y. in 1856.)

potato-blight caused the famine in Ireland in 1846–1847 William Robert Prince, the fourth proprietor of the famous Prince nurseries at Flushing, Long Island, paid $600 for less than a pint

[1] Called also Cinnamon Vine and Chinese Yam. *Cf.* foot-note 3, p. 734.

of small tubers of this plant for the purpose of ascertaining whether it could be substituted for the potato.

The wild yam-root (*D. villosa*) is found in moist thickets from New England to Florida and westward to Ontario, Minnesota, Kansas, and Texas.

The *Bloodwort Family* (Haemodoraceae), of some 9 genera and 35 species, is found chiefly south of the equator. The Red-roots (*Lachnanthes* and *Lophiola*[1]) have been described from eastern North America.

The *Amaryllis Family* (Amaryllidaceae) comprise bulbous, perennial, scape-bearing herbs, with regular or nearly regular flowers, with the parts in sixes. The tube of the six-parted corolla-like perianth is adherent to a 3-celled ovary. The 70 or more genera and 800 species occur wild chiefly in the warmer regions of the world. Those found in the temperate zones include Hymenocallis (*H. occidentalis*), Narcissus or Daffodil, and Jonquil, the Star grass (*Hypoxis*), and other species. Among cultivated genera are also *Amaryllis*, a bulbous plant from the Cape of Good Hope, and *Hippeastrum*, often included in trade catalogs under the name *Amaryllis*. The latter genus has a solid scape, and no scales between the filaments, while *Hippeastrum* has a hollow scape and small scales between the six distinct filaments.

The genus *Crinum* is closely related to *Amaryllis*, and is distinguished from the latter by having a longer perianth tube, and otherwise. The Swamp-Lily, of Georgia, Florida, Louisiana, and Texas, is *Crinum Americanum* L.

The distinguishing feature of *Narcissus* is that the flowers, borne on leafless scapes, have the perianth-tube prolonged at the base of the spreading lobes so as to form a more or less conspicuous *corona* or crown. The best known forms are the Daffodil or Trumpet Narcissus (*N. Pseudo-Narcissus* L.), the Paper-white Narcissus (*N. Papyraceus*), Poet's Narcissus (*N. poeticus* L.) (Fig. 636), the Jonquil (*N. Jonquilla* L.), and Bulbocodium or Hoop-Petticoat Daffodil (*N. Bulbocodium* L.). The Jonquil is distinguished from the common Daffodil, and the Poet's Narcissus by its rush-like leaves and by having its flowers in a cluster of 2–6 at the summit of the scape, the segments of the corolla scarcely over-

[1] *Lophiola* is placed by some authors in the Amaryllis Family.

lap, and the crown is *very short* (about $\frac{1}{8}$ in. long) and of the same color as the segments.

In this family also belongs the Century Plant or American Aloe (*Agave americana*), native of Central America and Mexico and

FIG. 636.—Poet's Narcissus (*N. poeticus*).

naturalized in the dry soil of Texas and Florida. They are known locally as "magueyes."[1] There are fully 300 species. The plant does not flower until after several (usually six or seven)

[1] They are also known as American Aloe, but are not be confused with the genus *Aloe*, of the Lily Family.

years' growth; the name "Century" plant, therefore, is quite misleading in this respect. The flowers grow in spikes or panicles at the ends of branches borne at the summit of a very rapidly growing, fleshy or fibrous scape that often attains a height of 15–20 feet. As the flowers begin to wither, buds form at the axils of the flower-stalks and develop into young plantlets, which fall to the ground and thus propagate the species vegetatively (Fig. 637).

Fig. 637.—Century Plant (*Agave* sp.). Young plantlets have taken the place of the flowers in the inflorescences.

In the north the genus is used only for decoration, but in its native regions it has large economic importance, some species furnishing fibre, and others soap. It is said that strips of the flower stalk of *A. americana* will serve as razor strops. The two chief intoxicating drinks of Mexico, Mescal and Pulque, are made from the juice of species of *Agave*. Pulque is the fermented juice of *A. atrovirens*, and other species; Mescal is distilled chiefly from the juice of an unknown species.

The commercially most important Agave is the Sisal Hemp or Henequen (*Agave sisalana* (Engelmann) Perrine; *Agave rigida* var. *Sisalana*), a native of the peninsula of Yucatan, but found also throughout Central America and the West Indies where it is extensively cultivated (Fig. 638). The fibro-vascular bundles of the thick, fleshy leaves furnish the rope-fibre. The leaves are 4–5 feet long, about 4 inches wide, and ½ inch thick. The pulp of the leaf is removed by machine-tools. The fibre is second only in strength and value to that obtained from Manila hemp (cf. p. 907).

Sisal and Manila hemp (a species of banana) are the chief sources of binder twine used in the harvesting of grains.

Agave decipens Baker, "false sisal hemp," found wild on the Florida coast and Keys, also yields a fibre, but of inferior quality. This species is easily distinguished from *A. rigida* by its spiny leaf margin, that of *A. sisalana* being entire, or nearly so.

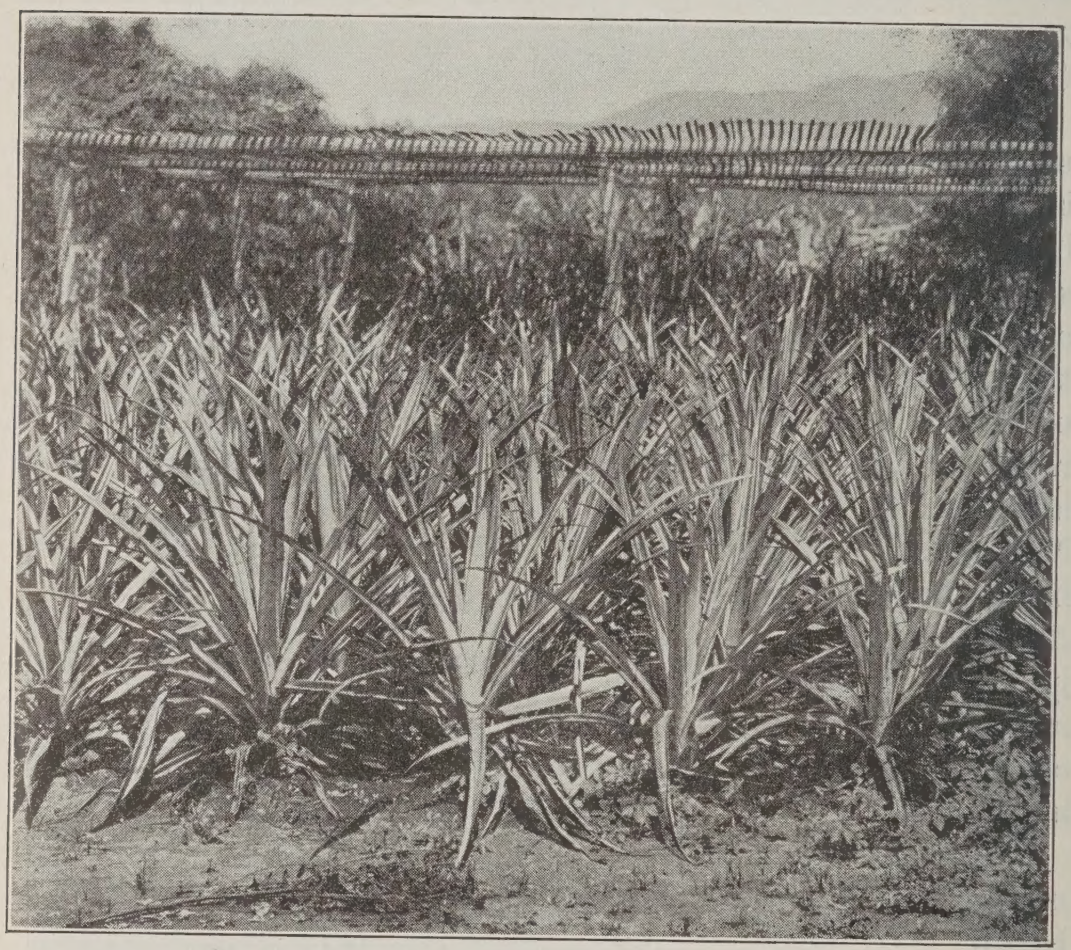


FIG. 638.—Sisal Hemp, or Henequen (*Agave sisalana*). (Bur. Sci. Manila, P. I.)

The *Iris Family* (Iridaceae) contains about 57 genera and 1000 species. Here belong the Blue-eyed-Grass (*Sisyrinchium*) containing more than 50 species, several of which are common in the United States, and the genus *Iris*, comprising about 150 species confined largely to north temperate regions. There are about 20 species in North America, of which the larger Blue Flag (*Iris versicolor*) is indigenous. The Yellow Flag (*I. Pseudacorus*)

has been naturalized in New England, New York, and New Jersey from Syria and the Barbary States.

The Family includes only herbs, which have a creeping rhizome (or tubers or corms), erect stems, erect or ascending, equitant, 2-ranked leaves, and regular or irregular perfect and showy flowers, either terminal or panicled, arising from a spathe of two or more leaves or bracts. The perianth is composed of six segments (clawed in *Iris*), 3 petals, and 3 petal-like sepals, convolute in the bud, and which are united below into a tube adnate to the 3-celled ovary. Alternating with the petals are three distinct or monadelphous stamens, with anthers facing outward (*extrorse*). The style is commonly 3-cleft. In the genus *Iris* the three petal-like divisions of the style are over the stamens, and bear the stigmas on the underside of their tips, which are commonly two-lobed. The fruit is an oblong or oval, 3–6 lobed capsule, containing many seeds.

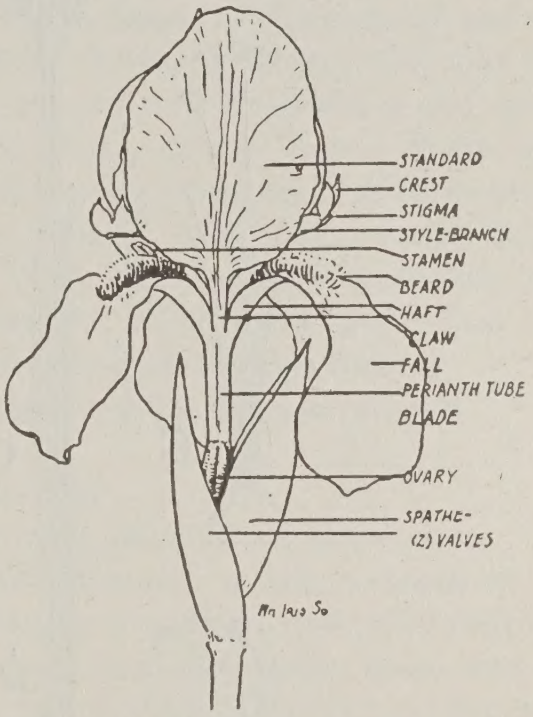


FIG. 639.—Iris. The parts of the flower. (After John S. and Grace W. Crooks.)

IRIS

The genus *Iris* is a large one, with the numerous species widely distributed throughout the north temperate zone. In horticultural literature the sepals are called *falls*, and the petals *standards* (Fig. 639). Inside the standards, and alternating with them, are three broad petal-like styles, each terminating in a characteristic crest. At the base of each style (on its lower face) is the scale-like stigma, only its lower surface being stigmatic. The perianth tube is more or less prolonged beyond the ovary. The flower stalk bears one to many flowers, and each of the flat, sword-like leaves is folded back on itself as so to form a flattened "pitcher." The name is from the Greek word (ἶρις), meaning rainbow. The genus is divided into two main groups, with subgenera, as follows:

I. Those with a rhizome (Rhizomatous). Sub-genera: *Evansia, Pogoniris, Pseudoregellia, Regellia, Pardanthopsis, Oncoyclus, Apogon.*

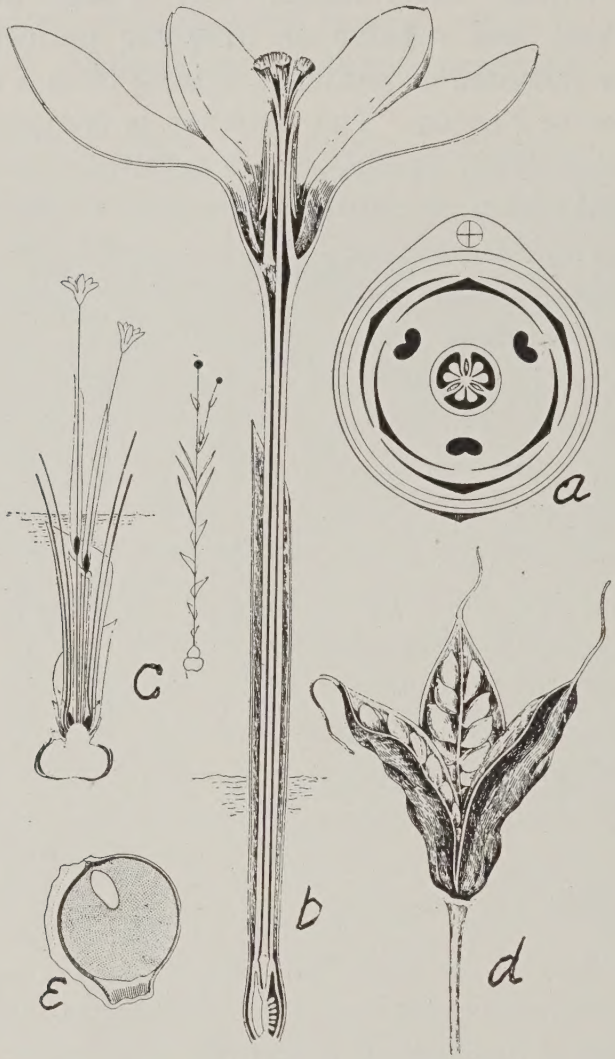


FIG. 640.—*Crocus vernus.* Flower in median longitudinal section; ground plan of flower; schemes of flowering shoot; dehiscing fruit; and section of the seed in the plane of the raphe. (After A. H. Church. Courtesy Clarendon Press.)

II. Those with a bulb (Bulbous). Sub-genera: *Juno, Xiphium, Gynandriris.*

The horticultural forms of *Iris* comprise about 700 named varieties, many of which are synonyms, *i.e.*, different breeders have given different names to the same variety. Orris root (*i.e.*, iris root) is prepared from the rhizomes of *I. florentina* and other species.

CROCUS

Among the early spring favorites of cultivated flowers is the genus *Crocus*. Some species are fall flowering. *Crocus* is the old Greek name, used by Theophrastus. The plants have a corm which sends up grass-like leaves, and showy flowers. The ovary and pod seldom rise above ground, the limb of the perianth being raised above the leaves by the growth of the perianth-tube, which thus becomes very long and slender (Fig. 640). Flowers usually precede the leaves. The divisions of the perianth are all similar and petal-like, or, in some forms, the three inner may be somewhat smaller. The flowers open only in sunshine and close at night, remaining closed on dark, cloudy days. There are about 75 more or less variable species, common in southwestern Asia and the Mediterranean region. Many color-forms have arisen from hybridization. The covering of the corm may be either membranaceous or reticulate. The floral spathe may be one- or two-leaved, and always subtends but one flower.

The genus is divided botanically into 3 groups, as follows:

a. Style-branches entire.

b. Style-branches once divided.

c. Style-branches with several hair-like divisions.

Crocus sativus, from southern Europe, is the commonest of the fall-blooming species, and is the source of commercial saffron. This species has been cultivated from very early times and is described by Theophrastus.[1] Its cultivation is quite an industry in Italy, France, and Spain. The commercial saffron[2] is composed of the deep orange-colored stigmas, collected with part of the style, and dried. It takes over 4000 flowers to produce one ounce of saffron, which is an orange-red dye.

[1] Theophrastus. Enquiry into plants. Eng. translation by Sir Arthur Hort. Book VI, par. 8.

[2] The Greek word κρόκος (krokos) was used to designate saffron as well as the flower from which it is obtained.

CHAPTER XXXIX

MONOCOTYLEDONS (CONCLUDED)

ORDER, Scitaminales

The order Scitaminales includes only large herbaceous plants with irregular, asymmetrical flowers, and seeds with perisperm (often, but incorrectly, called endosperm—*Cf.* p. 354), or seedless. The fruit is a capsule (*e.g.*, *Canna*); a berry (*e.g.*, the banana), or a utricle (*e.g.*, *Thalia* and *Maranta* (Arrowroot). The leaves are pinnately veined. The Scitaminales and the remaining orders of Monocotyledons have an inferior ovary.

THE BANANAS

The family of greatest economic importance in this order is the *Musaceae*, which includes the various species of bananas. These plants are, in reality, large herbs, though they often attain tree-like proportions. The sheathing petioles overlap in a way to form a cylinder of concentric layers—the false stem. The outer sheaths protect the younger, inner leaves, and all, together, protect the young flower-stalk, bearing the terminal inflorescence, as it pushes its way up through the hollow, pseudo-stem. The true stem is underground—a tuberous rhizome. The food stored in the rhizome, as well as that supplied directly from the leaves, nourishes the flower-stalk and fruit, and also the suckers which produce the new shoots. Each shoot dies after bearing one bunch of bananas. If too many suckers are allowed to form, they deplete the nourishment from the rhizome and the result is the formation of fewer "hands" of bananas, or smaller fruit.

After a shoot has borne a bunch of bananas the nourishment it contains passes down to help nourish the young suckers; the leaves then dry up and the old shoot finally falls or, in cultivation, is cut away. Gradually the young suckers form their own rhizome, drawing on the nourishment that may remain in the old rhizome of the parent plant.

The flowers are borne in large, drooping clusters on fleshy axes, and each cluster is protected by a spathe-like bract (Fig. 641). As the ovaries begin to develop into fruit the bracts fall away.

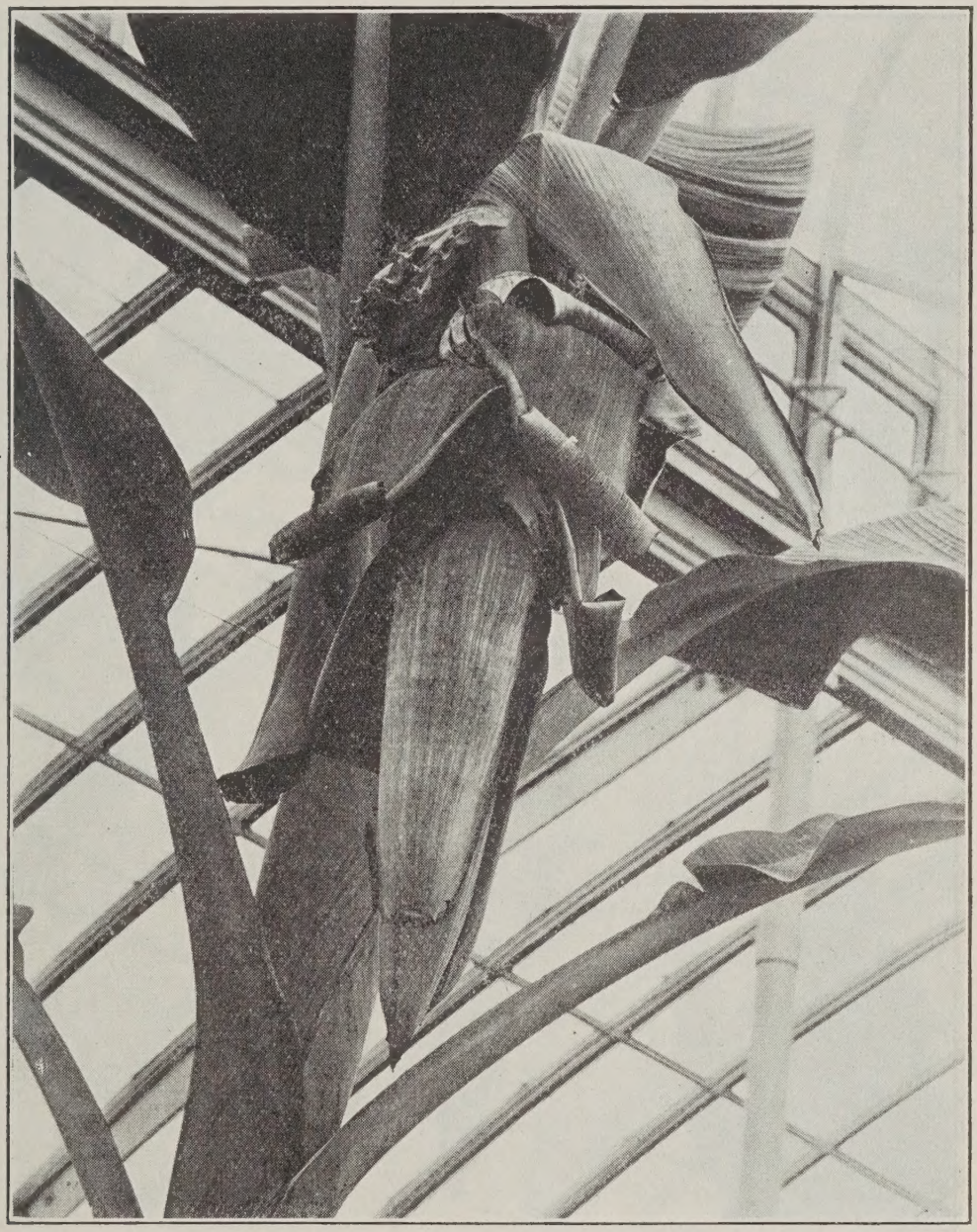


FIG. 641.—Banana (*Musa sapientum*). Early stage of inflorescence. The first bract has not yet fallen. Cf. Fig. 642.

This process proceeds from the base to the tip of the inflorescence (Fig. 642).

The flower is dorsiventral, the outer, anterior (abaxial) petal-like segment of the perianth commonly being larger than the

others. Five of the perianth-segments are connate, forming a tube at the base, and bearing five free tips. The two outer and the central tips represent the three sepals of the calyx; the other

FIG. 642.—Banana (*Musa sapientum*). Later stage with the fruit forming, and the sterile flowers still being uncovered at the distal end of the flower-stalk. Note the tearing of the leaf-blades. Cf. Figs. 32 and 641.

two tips represent two of the three petals. The calyx tip bears a minute appendage (Fig. 643, *F*, *a*). The free petal has an inflexed tip. This petal corresponds to the "lip" or labellum of the orchid

flower. The anthers do not always bear perfect pollen, and in *Musa sapientum*, one stamen (the posterior one) is always either sterile or absent, leaving only 5 stamens. In the Abyssinian banana (*Musa Ensete*) there are six functional stamens. The basal flowers of a cluster are pistillate (by the partial or complete abortion of the stamens); their ovaries are about ⅔ the total

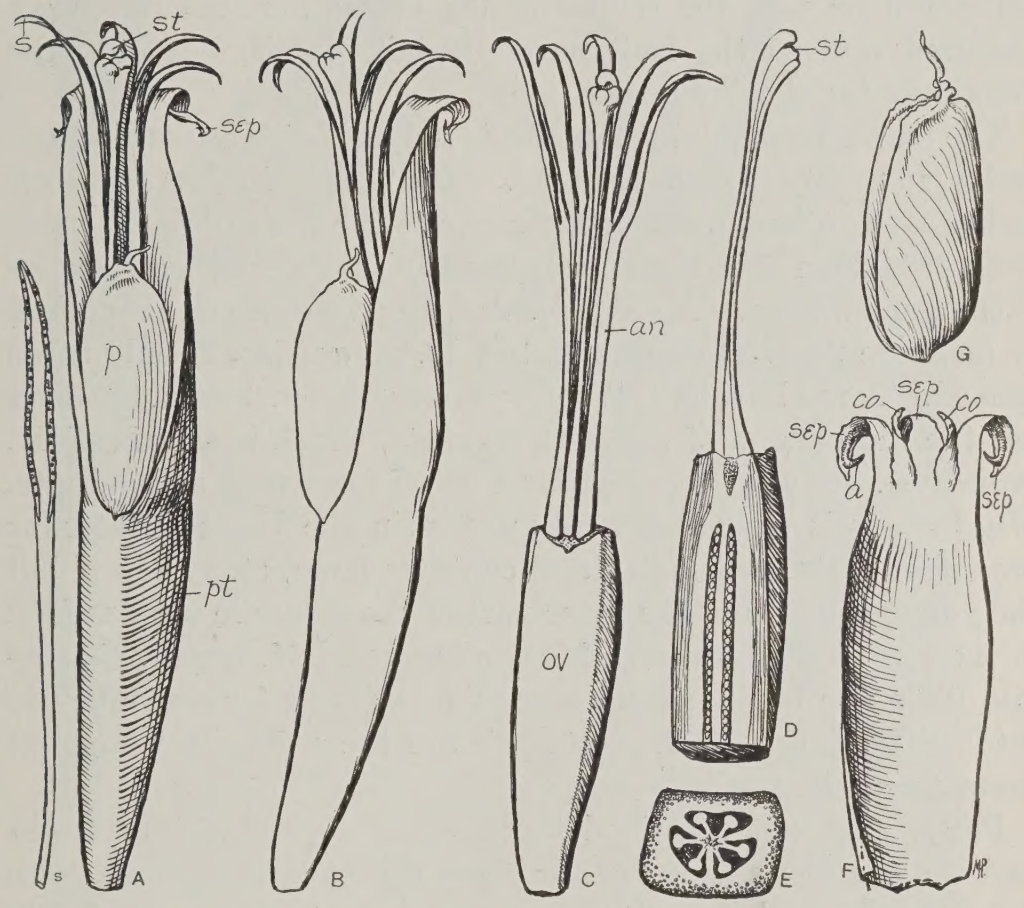


FIG. 643.—Banana (*Musa sapientum*). *A*, ventral or adaxial view of a flower; *B*, side view of flower; *C*, essential organs of a perfect flower (perianth removed); *D*, pistillate flower with perianth removed; *E*, cross-sectional view of the ovary, showing the ovules; *F*, upper (free) portion of the perianth tube; *G*, the free petal. *a*, appendage of calyx tips; *an*, anther; *co*, corolla tips of the perianth tube; *ov*, ovary, *p*, free petal; *pt*, perianth tube; *s*, stamen; *sep*, calyx lobes of perianth; *st*, stigma.

length of the flower, and it is these flowers that produce the fruit or bananas. Above these flowers is a region bearing either perfect flowers, or flowers with both essential organs imperfectly developed. These flowers have ovaries about ½ the total length of the flower. They form small, worthless hands. Flowers somewhat nearer the tip have ovaries about ⅓ the total length of the flower.

Finally, there are staminate flowers which, of course, do not form any fruit since they have no ovaries. The protection of the flowers by the bracts, and the fact that the pistillate flowers develop and are exposed by the opening of their protective bract before the male flowers on the same plant, tend to insure cross-pollination, which is accomplished by insects. But, whether pollinated or not, the ovules of the edible bananas never get fertilized and so the fruit never contains seeds, but only the remains of the aborted ovules.

The edible banana of commerce is the fruit of *Musa sapientum*[1] and is, in reality, a seedless berry. The "plantains," of the West Indies and other warm countries, are the fruit of *Musa paradisiaca*. These two sorts are generally considered as varieties of the same species. *Musa sapientum* may be eaten either cooked or (as more usually) uncooked, but *M. paradisiaca* is only eaten cooked. A red banana (*M. rubra*) grows wild in Tahiti. This is not the red banana of northern markets, which is a form of *M. sapientum*. *Musa Cavendishii* is a dwarf form with edible fruits. *Musa ensete* is more commonly grown in the United States for ornament. Its fruit is dry and contains large, stony seeds, but the young shoots and the inner part of the stem are used as food in the East. The fruits of *Musa glauca* and *M. nepalensis* contain little else but hard dry seeds "scarcely fir for a monkey to eat." The fibers of *Musa textilis* are the "Manila hemp" of commerce (Fig. 644).

Pliny, who first described the banana, says that the Greeks under Alexander saw it in India, and this country and southern Asia are generally considered as its home. It was probably

[1] The genus *Musa* is said by some writers to have been named by Plumier, a noted French Botanist (1646–1706), in memory of Antonius Musa, the brother of Euphorbus, physician to King Juba II of Numidia (about 25 A.D.), and after whom the genus *Euphorbia* is named. Musa was a freedman of the Emperor Augustus. Others derive the generic name *Musa* from *mauz*, the Arabic name for this plant. Gerarde, the herbalist, and other ancient authors, called it "Adam's apple," from the notion that it was the forbidden fruit of Eden; others have supposed it to be the "grapes," brought from the promised land by the spies of Moses.

The specific name, *sapientum*, means "of the wise"—the good judges, the connoisseurs, but this name probably harks back to the days when the sages of India "reposed beneath its shade and ate its fruit" (*Watt*). *Musa sapientum* L. = *M. paradisiaca*, sub-species *sapientum* L. (Otto Kunze).

introduced into the New World through San Domingo and Brazil by the Spanish and Portuguese. This is one of the most useful genera of plants in the world, the fruit taking the place of bread

FIG. 644.—Field of Manila Hemp (*Musa textilis*), in the Philippine Islands. (From Philippine Bureau of Science.)

and potatoes in some countries, the yield being large per acre. It is also the source of a medicine, and of a fermented drink (*Vino di banana*). The flower-heads of several species are eaten cooked, as is also the inner part of the stem, a half ton of the latter being

sold daily in Calcutta. The shoots or suckers and the tops of young plants are also eaten by both man and beast, and the outer sheaths or bracts of the inflorescence are given as fodder for elephants. Paper and cloth, as well as cord, are made from the fiber.

One writer states that the number of cultivated varieties is "infinite," and another likens it, in this respect to the apple. There are said to be sixty distinct kinds (under five species)

FIG. 645.—Ginger (*Zingiber officinale*). Plant, flowers, and bulbils. Note the one functional stamen at *k*. Cf. Fig. 646. (After Baillon.)

grown in India, and as many as eighty varieties in Batavia. This tendency to wide variation is evidence that reproduction is sometimes by seed, and numerous instances are on record of the abnormal formation of seed in the normally seedless fruit of the edible bananas.

A stalk of *M. sapientum* bears only one "bunch" of bananas, and the ovaries near the distal end of the inflorescence do not, as a rule, develop into edible fruit. The ripened bunch contains

200–300 bananas and may weigh as many pounds.[1] Shipment to northern markets is possible only by cutting off the bunch when the fruit is still green. Correlated with the enormous weight of material in the fruit is the unusually large leaf-area, which exposes a great amount of photosynthesizing tissue to the sunlight. The photosynthate, as elaborated, and also the food stored in the rhizome, passes to the inflorescence and is mostly stored in the enlarging ovaries. The leaves lack the marginal veins of some plants, and the holes and natural incisions of *Monstera* (p. 874); the lack of these features, combined with prominent lateral veins (pinnate venation) render the leaves easily torn by the wind (Figs. 32 and 644).

Fig. 646.—Ginger-Lily (*Hedychium coccineum*). Inflorescence. Note the one prominent functional stamen. Cf. Fig. 645.

Most of the stomata are on the under side of the leaf-blade. In hot, dry weather the halves of the blade fall together, thus helping to retard loss of water by transpiration. In cooler, humid weather the halves bend up, so that the upper surface of the leaf may become concave.

The Ginger Family (*Zingiberaceae*), contains *Zingiber officinale* (commercial ginger) (Fig. 645), *Eletteria Cardamomum* (the fruits of which are small or true Cardamon seed), *Amomum Cardamon* (which produces the large Cardamon seed), *Curcuma angustifolia* and *C. leucorrhiza* (the starchy roots of which yield the "arrow-root" starch of the East Indies), and the Ginger-Lily

[1] Bananas produce about 242,000 lbs. per acre; potatoes, 4000 lbs; and wheat only 2000 lbs.

or Garland Flower (*Hedychium*). Of the six stamens only the posterior one of the inner three is functional (Fig. 646). In *Hedychium* the staminodia are broad and petal-like; in *Zingiber* they are rudimentary. All the genera are tropical.

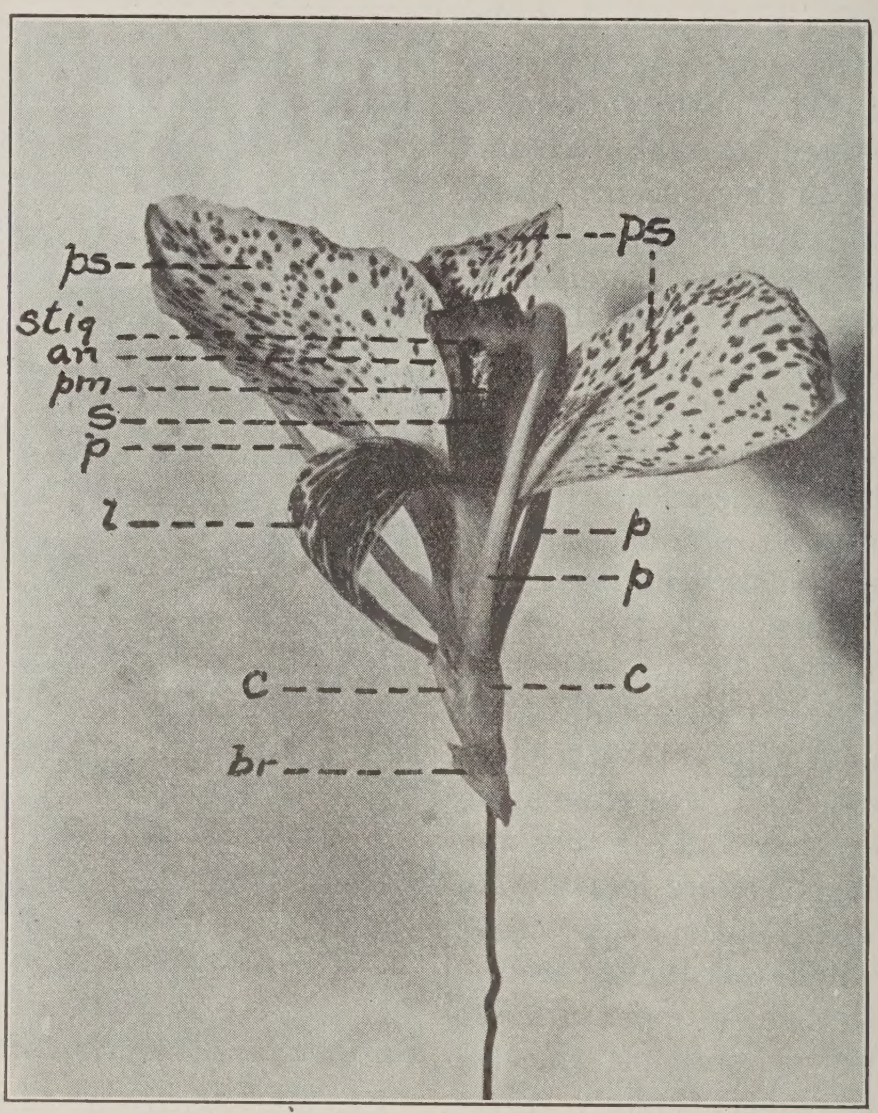


FIG. 647.—Canna flower, Variety "Gladiator." *An*, anther, which, in the bud was folded around and pressed against the surface of the flat style; *br*, bracts around the inferior ovary; *c*, calyx lobes (sepals); *l*, labellum or lip, which is one of the four petal-like staminodia; *p*, petals; *pm*, pollen-mass left on the style below the stigma when the anther was removed by the unrolling of the stamen; *ps*, the other three petal-like staminodia; *s*, style, stigmatic at the tip; *stig*, stigma at the tip of the style.

The Canna Family (*Cannaceae*) is best known by the numerous horticultural forms of *Canna*. These are perennial herbs with an irregular flower of interesting structure. The parts are, of

course, in threes, and the ovary is inferior. The flower is asymmetrical. As in the related Ginger Family, only one of the stamens bears an anther; the others are transformed into petal-like staminodia, one of which, larger than the others and reflexed, is the *labellum* (Fig. 647). The seeds, without endosperm, are numerous in *Canna*, but only one to each of the three locules in other genera.

The three styles (in *Canna*) are united into one strap-shaped organ, with a stigmatic surface near the tip. In the bud the staminodium is wrapped around the style and, when it becomes unwrapped, as the flower-bud opens, the pollen is left adhering to the side of the style *opposite to the stigmatic surface*. Cross-pollination is accomplished by bees. The insect, in search of nectar, alights on the labellum. This is sensitive, and when touched by the insect (or by the finger or any other object) it shortly bends down. This brings the bee so low that, when he thrusts his head into the perianth, it rubs against the pollen mass (Fig. 647) previously deposited on the style by the unwinding stamen, and his head becomes covered with pollen. When he alights on another flower, and again thrusts in his head, some of the pollen from the first flower is rubbed off onto the stigma of the second before the labellum bends down; this accomplishes cross-pollination. The plan does not always work perfectly, so that self-pollination often results.

A species of another family (*Marantaceae*), *Maranta arundinacea*, is the chief source of the West Indian arrowroot. Arrowroot is also obtained from several species of *Canna*.

THE ORCHIDS

At the apex of the monocotyledonous orders stands the *Orchidales*, of which the family *Orchidaceae* is the best known and most important. This large family is, by some authors, divided into Tribes, such as the *Cypripedieae* (the Lady's slippers); the *Ophrydeae* (*Orchis* and *Habenaria*); *Neottieae* (*Pogonia*, *Calopogon*, *Arethusa*, *Spiranthes* (Ladies' Tresses), and *Epipactis* (Rattlesnake Plantain), and others; and *Epidendreae* containing the Coral Root (*Corallorrhiza*), *Cattleya*, and numerous other genera.

With the exception of *Vanilla*, orchids are cultivated chiefly for the beauty of their flowers. The more common genera cultivated by florists include *Angraecum*, *Bulbophyllum*, *Calopogon*, *Catasetum*, *Cattleya* (Fig. 648), *Cypripedium*, *Dendrobium*, *Laelia*, *Masdevallia*, *Odontoglossum*, *Oncidium*, *Pogonia*, *Spiranthes*, and numerous others.

Darwin's Description of an Orchid Flower.[1]—In his classical book on the fertilization of orchids Darwin gives the following description of the structure of an orchid flower:

"The result of my dissections is given in the following diagram (Fig. 648). The fifteen little circles represent so many groups

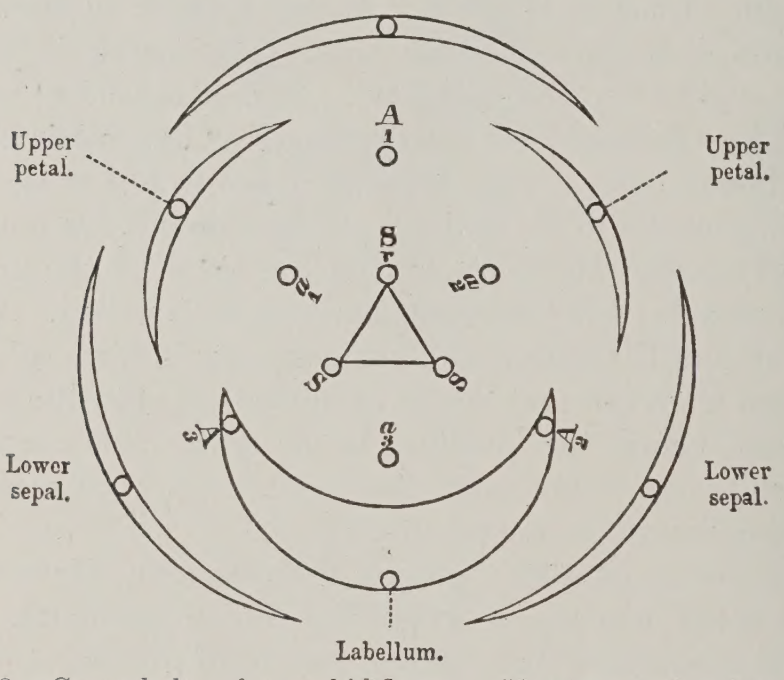


FIG. 648.—Ground plan of an orchid flower. *SS*, stigmas; *Sr*, stigma modified into rostellum; *A*1, fertile anther of the outer whorl; *A*2, *A*3, anthers of the same whorl combined with the lower petal, forming the labellum; *a*1, *a*2, rudimentary anthers of the inner whorl (fertile in *Cypripedium*), generally forming the *clinandrium* or cavity in the apex of the column between the anther sacs, which often contains the stigmatic surface; *a*3, third anther of the same whorl, forming, when present, the front of the column. (After Darwin.)

of spiral vessels, in every case traced down to one of the six large ovarian groups. They alternate in five whorls, as represented; but I have not attempted to give the actual distances at which they stand apart. In order to guide the eye, the three

[1] Darwin, Charles. The various contrivances by which orchids are fertilized by insects. Second Edition, Revised. New York, 1898.

central groups running to the three pistils are connected by a triangle.

"Five groups of vessels run into the three sepals together with the two upper petals; three enter the labellum; and seven run up the great central column. These vessels are arranged, as may be seen, in rays proceeding from the axis of the flower; and all on the same ray invariably run into the same ovarian group; thus the vessels supplying the upper sepal, the fertile anther (A_1), and the upper pistil or stigma (*i.e.*, the rostellum S_r),

FIG. 649.—An orchid; form of *Cattleya Trianae*.

all unite and form the posterior ovarian group. Again, the vessels supplying, for instance, the left lower sepals, the corner of the labellum and one of the two stigmas (S) on the same side, unite and form the antero-lateral group: and so with all the other vessels.

"Hence, if the existence of groups of spiral vessels can be trusted, the flower of an Orchid certainly consists of fifteen organs, in a much modified and confluent condition. We see three stigmas, with the two lower ones generally confluent, and with the upper one modified into the rostellum. We see six stamens, arranged in two whorls, with generally one alone (A_1) fertile. In Cypripedium, however, two stamens of the inner whorl (a_1 and a_2) are fertile, and in other Orchids these two are represented more plainly in various ways than the remaining stamens. The third stamen of the inner whorl (a_3), when its vessels can be traced, forms the front of the column: Brown thought that it often formed a medial excrescence, or ridge, cohering to the labellum; or, in the case of Glossodia,[1] a filamentous organ, freely projecting in front of the labellum. The former conclusion does not agree with my dissections; about Glossodia I know nothing. The two infertile stamens of the outer whorl (A_2, A_3) were believed by Brown to be only occasionally represented, and then by lateral excrescences on the labellum; but I find the corresponding vessels invariably present in the labellum of every Orchid examined,—even when the labellum is very narrow or quite simple, as in Malaxis, Herminium, or Habenaria."

Of the wonderful variations and modifications or orchid flowers, Darwin wrote as follows:[2]

"It is interesting to look at one of the magnificent exotic species or indeed, at one or our humblest forms, and observe how profoundly it has been modified, as compared with all ordinary flowers,—with its great labellum, formed of one petal and two petaloid stamens,—with its singular pollen-masses, hereafter to be referred to,—with its column formed of seven cohering organs, of which three alone perform their proper function, namely, one anther and two generally confluent stigmas,—with the third stigma modified into the rostellum and incapable of being fertilised,—and with three of the anthers no longer functionally active, but serving either to protect the pollen of the fertile anther or to strengthen the column, or existing as mere rudiments, or

[1] See Brown's observations under Apostasia in Wallich's "Plantae Asiaticae rariores," 1830, p. 74.

[2] Darwin, *l.c.*, pp. 245–246.

entirely suppressed. What an amount of modification, cohesion, abortion, and change of function do we here see! Yet hidden in that column, with its surrounding petals and sepals, we know that there are fifteen groups of vessels, arranged three within three, in alternate order, which probably have been preserved to the present time from being developed at a very early period of growth before the shape or existence of any part of the flower is of importance for the well-being of the plant.

"Can we feel satisfied by saying that each Orchid was created, exactly as we now see it, on a certain "ideal type;" that the omnipotent Creator, having fixed on one plan for the whole Order, did not depart from this plan; that he, therefore, made the same organ to perform diverse functions—often of trifling importance compared with their proper function—converted other organs into mere purposeless rudiments, and arranged all as if they had to stand separate, and then made them cohere? Is it not a more simple and intelligible view that all the Orchideae owe what they have in common, to descent from some monocotyledonous plant, which, like so many other plants of the same class, possessed fifteen organs, arranged alternately, three within three in five whorls; and that the now wonderfully changed structure of the flower is due to a long course of slow modification,—each modification having been preserved which was useful to the plant, during the incessant changes to which the organic and inorganic world has been exposed?"

Speaking of one of the commonest genera carried by florists, Darwin said:[1]

"I will begin with the genus Cattleya, of which I have examined several species. These are fertilised in a very simple manner different from that in any British Orchid. The rostellum (r, Fig. 650, A, B) is a broad, tongue-shaped projection, which arches slightly over the stigma; the upper surface is formed of smooth membrane; the lower surface together with the central portion (originally a mass of cells) consists of a very thick layer of viscid matter. This viscid mass is hardly separated from the viscid matter thickly coating the stigmatic surface which lies close beneath the rostellum. The projecting upper lip of the anthers rests on, and opens close over the base of the upper membranous

[1] Darwin, *l.c.*, pp. 143–145.

surface of the tongue-shaped rostellum. The anther is kept closed by a spring, at its point of attachment on the top of the column. The pollinia consist of four (or eight in *Cattleya crispa*) waxy masses, each furnished (see Figs, C and D) with a ribbon-like tail, formed of a bundle of highly elastic threads, to which numerous separate pollen-grains are attached. The pollen therefore

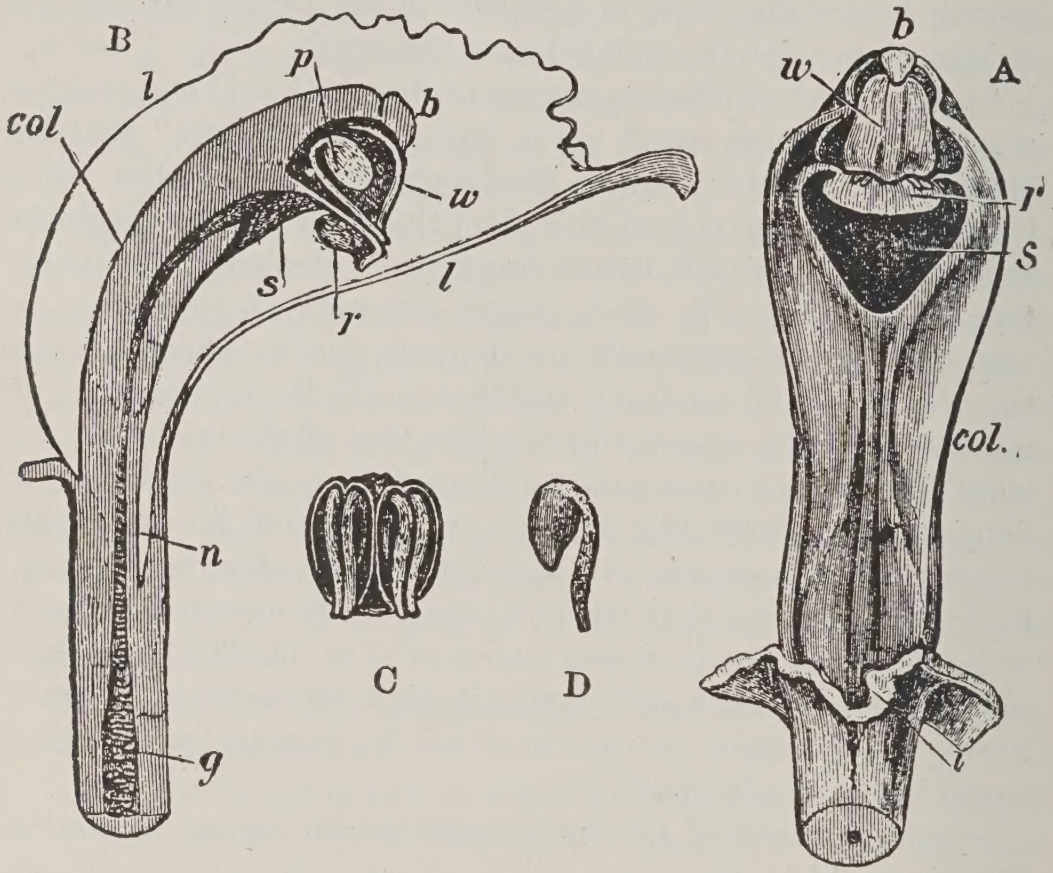


FIG. 650.—*A*, front view of column, with perianth removed; *B*, median longitudinal section of the flower, with sepals and petals removed, except the bisected labellum, shown in outline; *C*, anther viewed on the under side, showing the four candicles with the four pollen-masses beneath; *D*, A single pollinium, side view, showing the pollen-mass and caudicle. *a*, anther; *b*, spring at the top of the column; *p*, pollen-masses; *r*, rostellum; *s*, stigma; *col.*, column; *l*, labellum; *n*, nectary; *g*, ovarium or germen. (After Charles Darwin.)

consists of two kinds, namely, waxy masses and separate though compound grains (each, as usual, consisting of four) united by elastic threads. This latter kind of pollen is identical with that of *Epipactis* and other Neottieae. These tails, with their appended pollen-grains, act as caudicles, and are thus designated, for they serve as the means for the removal of the larger waxy masses from the anther-cells. The tips of the caudicles are

generally reflexed, and in the mature flower protrude a little way out of the anther-case (see Fig. A) lying on the base of the upper membranous lip of the rostellum. The labellum enfolds the column, making the flower tubular, and its lower part is produced into a nectary, which penetrates the ovarium.

"Now for the action of these parts. If any body of size proportional to that of the tubular flower be forced into it—a dead humble-bee acts very well—the tongue-shaped rostellum is depressed, and the object often gets slightly smeared with viscid matter; but in withdrawing it, the rostellum is upturned, and a surprising quantity of viscid matter is forced over the edges and sides, and at the same time into the lip of the anther, which is also slightly raised by the upturning of the rostellum. Thus the protruding tips of the caudicles are instantly glued to the retreating object, and the pollinia are withdrawn. This hardly ever failed to occur in my repeated trials. A living bee or other large insect alighting on the fringed edge of the labellum, and scrambling into the flower, would depress the labellum and would be less likely to disturb the rostellum, until it had sucked the nectar and began to retreat. When a dead bee, with the four waxy balls of pollen dangling by their caudicles from its back, is forced into another flower, some or all of them are caught with certainty by the broad, shallow, and highly viscid stigmatic surface, which likewise tears off the grains of pollen from the threads of the caudicles.

"That living humble-bees can thus remove the pollinia is certain. Sir W. C. Trevelyan sent to Mr. Smith of the British Museum a *Bombus hortorum*, which was forwarded to me—caught in his hothouse, where a Cattleya was in flower—with its whole back, between the wings, smeared with dried viscid matter, and with the four pollinia attached to it by their caudicles, ready to be caught by the stigma of any other flower if the bee had entered one."

In many orchids ovules are not formed until after pollination has taken place.

According to the mode of growth of their stems, orchids fall into two groups, *monopodial* and *sympodial*. In the former, growth in length is continued indefinitely by a terminal bud. Lateral branches may arise but they are always secondary in

size and importance to the main stem. They may vary in size from climbing vines (*Renanthera*) which may become twelve feet long, to such forms as *Polyrrhiza funalis*, in which the stem never develops beyond the stage of a scaly bud. In the absence of a leafy stem the function of photosynthesis is performed by the chlorophyll-bearing roots.

FIG. 651.—An orchid (*Dendrobium nobile*), showing aerial roots, covered with white velamen.

In sympodial orchids each shoot continues to grow for only one or two years, growth being continued by new shoots which arise in the axils of scale-like leaves at the base of the original main stem. Each new shoot is at first prostrate, often underground, and is called the rhizome. In climbing, sympodial orchids, like *Vanilla* (Fig. 658), branches may originate in the axils of the leaves. The habit of the rhizome—whether long (*Epidendrum*) or short (*Cattleya*), determines in large measure the appearance of the plant. The orchids are all herbs.

Orchid Roots.—The roots of orchids afford an interesting illustration of the adaptation of an organ to various conditions of environment. Those forms, like *Cypripedium*, *Spiranthes*, and others, which grow in the soil, have, of course, the normal type of terrestrial roots, with root-cap, and zone of root-hairs

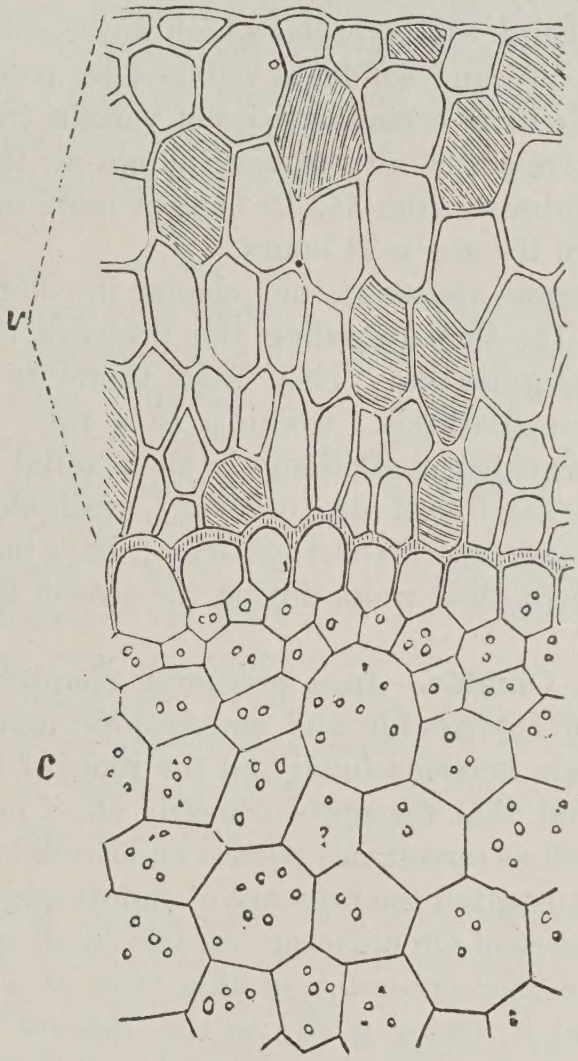


FIG. 652.—Cross-section of an air-root of an orchid. *c*, cells of the cortex; *v*, velamen. (After Unger from Vines.)

which absorb water from the soil. But many orchids, especially in the tropics, are epiphytes, growing on the trunks and branches of trees. These forms, of course, have no need of soil-roots, but develop a type of *aerial roots* (Fig. 651), which have a variety of functions. In the first place they may serve to fasten the orchid to the plant or other support on which it grows. They

possess a layer of spirally thickened cells (tracheids), which are filled with air (Fig. 652). When dry this layer, called the *velamen*,[1] appears white, and often papery, and in times of drought it serves to retard or prevent the loss of water by evaporation from the roots. In some species the velamen is covered with innumerable fine hairs which give a velvety surface.

On the other hand, this layer has a high water-absorbing capacity, and can absorb and condense water-vapor from the air. It is said that if plants of certain species of various tropical orchids are transferred from very dry to very humid air the velamen of their roots will absorb from 8% to 11% or more of their weight of moisture from the air in 24 hours.

When aerial roots are moist they change in color from papery white to greenish, thus revealing the presence of chlorophyll in the underlying tissues. They may therefore perform the function of photosynthesis. Orchids, as a rule, prefer plenty of light and this chlorophyll tissue in their aerial roots enables them to make the fullest use of every available ray. Some orchids, indeed (*e.g.*, species of *Angraecum*), have no other chlorophyll tissue except their roots during the season when they are not in flower.

Symbiosis in Orchids.—In a preceding chapter (p. 214) we have learned of ectotrophic and endotrophic mycorrhizas, the symbiotic relation between fungi and the roots of higher plants. It has been fond that the roots of nearly all, if not all, orchids (epiphytic as well as terrestrial) possess endotrophic mycorrhizas. Wahrlich[2] demonstrated the presence of endotrophic mycorrhizas in some 500 species of Orchidaceae—in fact in all species that he studied. The earlier observers of this were at a loss to know how to interpret it, owing partly to the unusual nature of the phenomenon and partly to the limitations of their microscopes and their technique. Schleiden thought the filaments were a part of the tissue of the orchid; Schacht believed that they were true fungal threads, but that they occupied only the dead cells of the root. The French botanist Prillieux, in a thorough study of the Bird's-Nest Orchid (*Neottia Nidus-avis*), in 1856, was

[1] Latin *velámen*, a sheath.

[2] Wahrlich, Beitrag zur Kentniss der Orchideen Wurzelpilze. *Bot. Zeit.* **44**: 481. 1886.

among the first to demonstrate that the filaments were, as Schacht believed, mycelium of a fungus, and that they penetrated the orchid cells while the latter were still living (Fig. 653). Later studies, culminating in the brilliant researches of Noël Bernard, have only served to confirm the fact that all orchids, wild or cultivated, have endotrophic[1] mycorrhizas in their roots and rhizomes. Guignard showed that the aerial roots of epiphytic orchids, such as Vanilla and others, do not possess mycorrhizas but soon acquire them when brought into contact with infected soil.

Certain species such, for example, as the coral-root orchid (*Corallorhiza*), *Epiphyllum*, and *Epipogon aphyllus*, illustrate a condition where the root-system has been completely atrophied, and the lower part of the shoot (rhizome), infested with the mycorrhizal fungus, serves every purpose of the root, including anchorage and absorption. *Corallorrhiza* has been interpreted by Bernard[2] as representing a late stage in the evolution of symbiosis.[3]

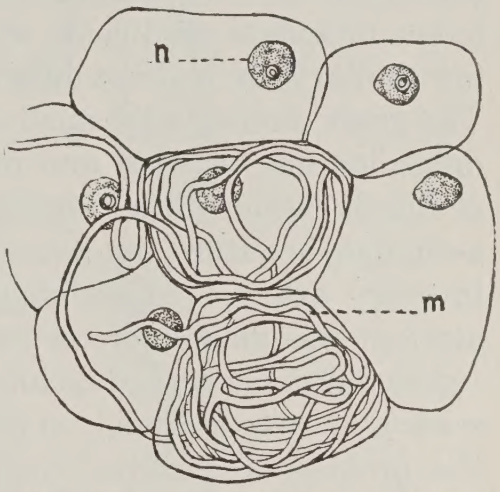


FIG. 653.—Portion of young cellular tissue of a root of the Bird's-Nest Orchid (*Neottia Nidus-avis*), containing filaments of an endotrophic fungus. *n*, cell-nucleus; *m*, mycelium of the fungus. (After Prillieux. Ann. Sci. Nat., 1856.)

Germination of Orchid Seed.—For many years the germination of orchid seed remained an unsolved problem. In 1832 seeds of *Prescottia plantaginea* were raised abundantly in the garden of the Royal Horticultural Society (London), but all record of the method employed appears to have been lost. In 1854 a foreman gardener by the name of Dominy, in the nursery of Messrs. Veitch, Exeter (England), obtained orchid seed by

[1] Also called endophytic (*within the plant*).

[2] Bernard, Noël. L'evolution dans la symbiose. Ann. Sci. Nat. Bot. 9th Ser. **9**: 1–92. 1909.

[3] It is of interest to note that, in another orchid, *Aeranthus*, evolution has operated in the opposite direction. Here all the organs of the shoot are suppressed except the flower, and the plant has been interpreted as a free-living root.

crossing *Calanthe Masuca* with *C. furcata*. The seeds were immediately sown, and in two years the hybrid seedling was in flower. In recognition of Dominy's success in raising hybrid orchids from seed as a horticultural practice Lindly named the hybrid *Calanthe Dominii*. The exact condition, however, essential to the germination of these seeds was not understood, or if so, was kept as a professional secret.[1]

Now the seeds of orchids, produced in great quantity, are extremely minute, commonly spindle-shaped bodies, with a loose, reticulate seed-coat, and a tiny embryo consisting of a few similar cells, and not differentiated into caulicle and plumule. The great number and small size of the seeds has favored their dissemination by wind and other agencies, so that orchids are of almost cosmopolitan distribution. These seeds must, of course, germinate in nature, but botanists and horticulturists were baffled in every attempt to germinate them artificially, although the attempt was made more or less continuously from the year 1802 (when Salisbury argued deductively that nature would not make seeds that were incapable of germination) to the year 1899, when the problem was solved (inductively) by the French botanist, Noël Bernard.[2]

One fact had been recognized for some time, namely, that whenever germination was secured it was by sowing the seeds on the surface of the soil of the pot containing the parent plant, or on

[1] Between 1854 and 1880 Dominy produced some 25 hybrids of orchids. For his skill and success he was, in the latter year, awarded a medal by the Royal Horticultural Society.

[2] It is instructive to note how easily *deductive* reasoning (*i.e.*, reasoning from general principles, assumed to be true, to particular cases) may lead one into error in science, especially if the inference thus reached is not thoroughly tested and verified by observation and experiment. It is easy for anyone to ascertain that "nature" very commonly makes seeds (or, more accurately speaking, seed-like bodies) that are incapable of germination. The *inductive* method used by Bernard (supplemented of course by deduction) is the only sure road to truth in scientific work.

It is very interesting to note, in this connection, how another method of reasoning, namely, by *analogy*, is very liable to lead one straight to error. Hieronymus Tragus (*Cf.* p. 562), an early German botanist, observed that, after an orchid has flowered, a fine dust was shed from what is left of the flower, but he believed it to be merely the dust of the dried capsule. Noting that some orchid flowers resemble birds, he attributed their origin to birds, since (as he supposed) they did not produce seed!

soil in which the given species of orchid had grown. Finally, in 1899, Bernard found a plant of the epiphytic Bird's-Nest Orchid (*Neottia Nidus-avis*), which had fallen to the ground the preceding fall and was buried under a layer of dry leaves. In the spring the seeds, still inclosed in the capsules, had germinated in great

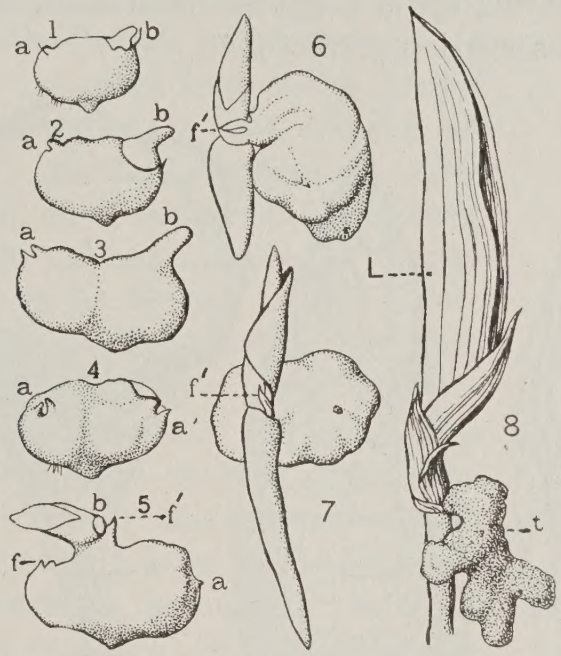


FIG. 654.—Germination of the seed of an orchid (*Angraecum maculatum*). 1, seedlings with two buds, one of which, *a*, terminates an axis that may become tuberized, the other, *b*, will develop into a leafy stem. 2–3, seedlings a little more advanced than 1. 4, seedling older than 3, but where the two axes, terminated by the buds *a* and *a'*, will remain tuberous. 5, seedling farther developed. One of the axes, *a*, is tuberous; the other, *b*, tuberous at its base, has developed a stem from its second leaf. The first leaf, *f*, which has a bud in its axil, has been repressed by the growth in size of the stem in the axil of the leaf, *f'*. Below the leaf *f'*, enveloped in a sheath, one may see a small papilla, the rudiment of a root. 6, seedling still farther developed. The root has grown considerably, and in elongating has pushed to one side the leaf *f*. 7, seedling still further advanced. The root has elongated, and the first leaf-sheath, *f'*, is partly destroyed. The summit of the fourth leaf-sheath shows below the third. 8, plant farther developed. The perfect leaf, *L*, has appeared within the leaf-sheaths. The tuberous axis has branched in such a way as to produce a lobed tubercle. (Redrawn from Prillieux and Rivière. Ann. Sci. Nat., 1856.)

numbers so that he could observe the stages of germination from the beginning until the seedling was 5 mm. long. Microscopic examination of a cross-section of a very young seedling showed three layers of cells, as follows: 1. At the center small parenchyma cells; 2. Next several layers of cells almost completely filled with a compact ball of fungus-filaments (mycelium); 3. The

outer layer of epidermal cells without starch or mycelium. Bernard was also impressed with the fact that the fungus-filaments were present in *all* stages, from the seeds just beginning to germinate up to the seedlings and the mature plants.[1] Prillieux had, in 1856, observed the mycelium in the roots of orchids, and also in germinating seeds (Figs. 654 and 655), but he failed to interpret his observation correctly.[2]

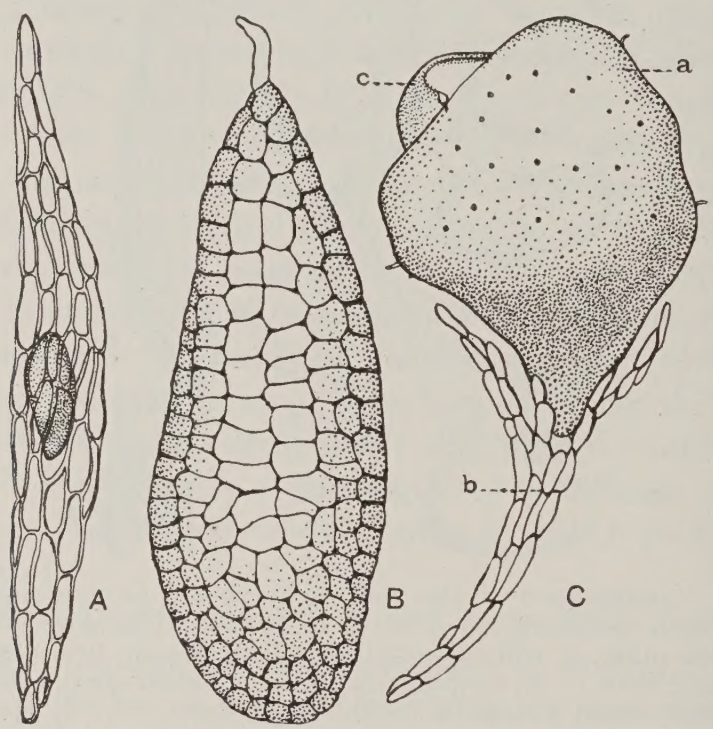


FIG. 655.—Structure and germination of the seed of an orchid (*Angraecum maculatum*). *A*, seed, much enlarged, with embryo showing within the seed-coat; *B*, embryo, removed from seed and greatly enlarged. It is only an undifferentiated mass of cells; *C*, seed germinating. The embryo, *a*, is enlarged at its upper part, and in growing it has ruptured the seed coat. At the apex of the embryo may be seen a young bud. (Redrawn from Prillieux and Rivière. Ann. Sci. Nat., 1856.)

Bernard then entered upon the truly scientific plan of following up his observation in nature by a course of painstaking experi-

[1] Bernard, Noël. Sur la germination du *Neottia Nidus-avis*. Compt. Rend. Acad. Sci. Paris. **128**: 1253–1255. 1899.

[2] Prillieux, Ed. and Aug. Rivière. Observations sur la germination et le developpement d'une orchidee (*Angraecum maculatum*). Ann. Sci. Nat. Bot. 4 Ser. **5**: 117–136. 1856.

Prillieux, Ed. De la structure anatomique et du mode de vegetation du *Neottia Nidus-avis*. Ann. Sci. Nat. Bot. 4 Ser. **5**: 267–282. 1856.

mentation.[1] By sowing small fragments of an infected orchid root on suitably prepared sterilized agar in a test-tube Bernard ascertained that the fungus developed freely, and that it could be transplanted from tube to tube. Such pure cultures were continued for four years without returning the fungus to the orchid. In these cultures the fungi formed the characteristic balls observed in the cells of the infected root. Bernard recognized three species of fungi, all of the genus *Rhizoctonia;* some grow on various species of orchid, others appear to be limited to one or two species. The following is Bernard's own statement of his germination experiments:

"Although the fungi can live apart from their host-plants, the orchids themselves require the presence of their guests for their own development. I have sown the seeds of numerous orchids 'aseptically' in sterilized tubes, on cotton or in jelly, saturated with a nutritive solution. I have for many months protected the seeds under covers from micro-organisms in suitable temperature and light. In these conditions the seeds have not freely germinated; they swell, and later on they get green, but their growth remains insignificant.

"On the other hand, if germs of the appropriate fungus are sown with the seeds, they commence to germinate almost immediately in a very regular manner. With the fungi which I possess, I have obtained not only the germination of *Cattleya* and of *Cypripedium,* but also of *Odontoglossum,*

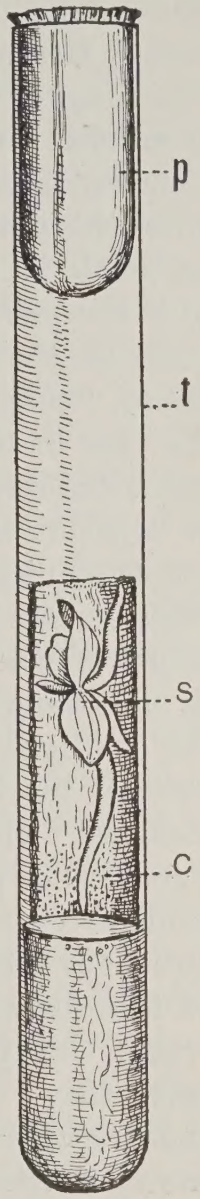


FIG. 656.—Seedling of an orchid grown by Bernard, on sterilized agar in a test-tube in contact with the germinating spores of a fungus. (After Noël Bernard. Redrawn from Costantin.)

[1] Bernard, Noël. Recherches Experimentales sur les Orchidees. Rev. Gen. Bot. **16:** 405–451; 458–476. 1904. *Ibid.* On the germination of orchids. Rept. 3rd Internat. Conference 1906 on Genetics, pp. 292–296. See also Denis. Orchid Rev. **17:** 156.

Phalaenopsis, and *Vanda,* which are regarded by practical men as more difficult."

One of Bernard's cultures is illustrated in figure 656.

The fungi of Cypripedium and of Cattleya kept cultivated on agar in tubes for three years lost their ability to cause the seeds of the corresponding species to germinate. But if a fungus which has lost this power is allowed to live for some time in the embryo of an orchid its ability of inducing seeds of that species to germinate is restored. "So as always to be able to produce a fungus suitable for the germination of orchids of a certain species," says Bernard, "cultures of the seeds of that species should be made every year in the laboratory, in order to maintain and even to increase the strength of the fungus in question, thus keeping it alive without interruption in the embryo, whence it may be taken as required."

Why Certain Orchids Grow in Colonies.—It is well known to students of wild flowers that various species of orchids always grow in colonies, single plants rarely, if ever, occurring. Ames made a special study of the Rattle-snake-plantain (*Epipactis pubescens*) for the purpose of explaining its habit of growing in colonies. He found the explanation in the method of the dispersal and germination of the seed. The ground in the immediate vicinity of growing plants is infested with a fungus essential for the germination of the seed. Seeds carried by the wind to a distance from the parent colony fall, in the majority of cases, on ground that lacks the necessary mycorrhizal fungus; they, therefore, fail to germinate. Ames sowed an abundance of the tiny seeds one autumn on the ground between plants of thrifty colonies, and the following August found hundreds of seedlings (protocorms), "for all the world similar to microscopical carrots in shape, although pure white in color, the smallest ones hardly a millimetre long . . . Microscopical examination of the tiniest protocorms revealed mycorrhizal infection. In embryos still partly enclosed by the testa of the seed the fungus extended nearly the whole length, but as growth progresses the upper half becomes translucent, free from hyphae, the cells containing starch-like granules . . . Through the long cobwebby hairs that arise single or in tufts, far apart on the surface of the protocorm, the fungal hyphae could be clearly seen

in their course from the interior of the protocorm to the humus from which, presumably, they help to bring in substances that the Orchid utilizes, and in exchange for which they may be supplied with something more than an abiding place."[1]

This dependence of the orchid seed on a fungus for germination is believed to explain, in part at least, why certain orchids are so rare in their native land; the chances of the seed finding conditions favorable to germination being slight. In this connection we may also realize the great advantage of the enormous quantity of seeds produced by most orchids. One capsule of a species of the orchid, *Maxillaria*, was found to contain 1,756,444 seeds. In the struggle for existence during the long course of evolution of seed-bearing plants, those individuals that bore great quantities of seed would stand much greater chances of having some of the seed fall on ground containing the necessary fungus; these individuals, then, would produce progeny inheriting this capacity for abundant seed production, while less prolific strains would die out.

Non-symbiotic Germination of Orchid Seeds.—In some of his experiments Bernard obtained the germination of seeds of species of two orchids—*Cattleya* and *Laelia*, without the intervention of a fungus. His experiments have been repeated and extended by Knudson,[2] whose results have led him to suggest "that germination is induced not by any action of the fungus within the embryo, but by products produced externally on digestion or secreted by the fungus". He has succeeded in germinating seeds of species of five or six genera without the aid or any fungus, provided certain sugars, such as glucose and particularly fruit sugar (fructose) are present. It would appear that the necessity of a fungus for the germination of orchid seed, at least in all cases, is not conclusively proved. The question should be studied further experimentally.

Vanilla.—Extract of vanilla, so commonly used for flavoring, is obtained from the pods of two species of orchids, *Vanilla planifolia* (indigenous in Mexico and Central America), and *V. pompona* (Mexican and West Indian species with shorter and

[1] Ames, Oakes. Seed dispersal in relation to colony formation in Goodyera pubescens. The Orchid Rev. **29**: 105–107. 1921.

[2] Knudson, Lewis. Nonsymbiotic germination of orchid seeds. Bot. Gaz. **73**: 1–25. Jan., 1922.

thicker pods). The former is the more important, and is now extensively cultivated in the old and new world tropics (Fig. 657).

The plant is a climbing epiphyte, with a long succulent green stem and fleshy leaves. The soil-roots penetrate only between

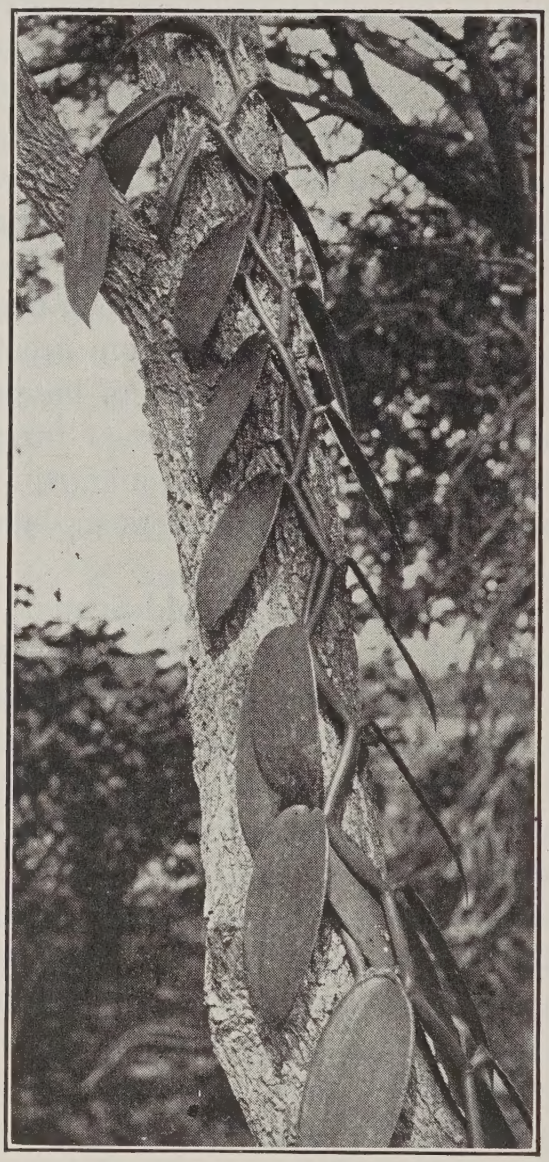


FIG. 657.—Vine of *Vanilla planifolia*, growing on a tree in Hope Gardens, Jamaica, W. I. (After Maxon, U. S. Dept. Agr.)

the surface layer of humus and the subsoil, hence the plant is called a "surface feeder." The aerial roots develop opposite the leaves and serve as tendrils, holding the plant to the trees or other supports on which it grows. The flower clusters are racemes in the axils of the leaves, two or three inches long, but

bearing flowers measuring as much as four inches across (Fig. 658). The early Spanish explorers found the Aztecs using vanilla for flavoring chocolate. It was introduced into Europe about 1510, and was first grown in England in the early part of the nineteenth century, where it first flowered and fruited in 1807. Plants sent from the Botanic Garden of Antwerp, Holland, in 1819, to Java

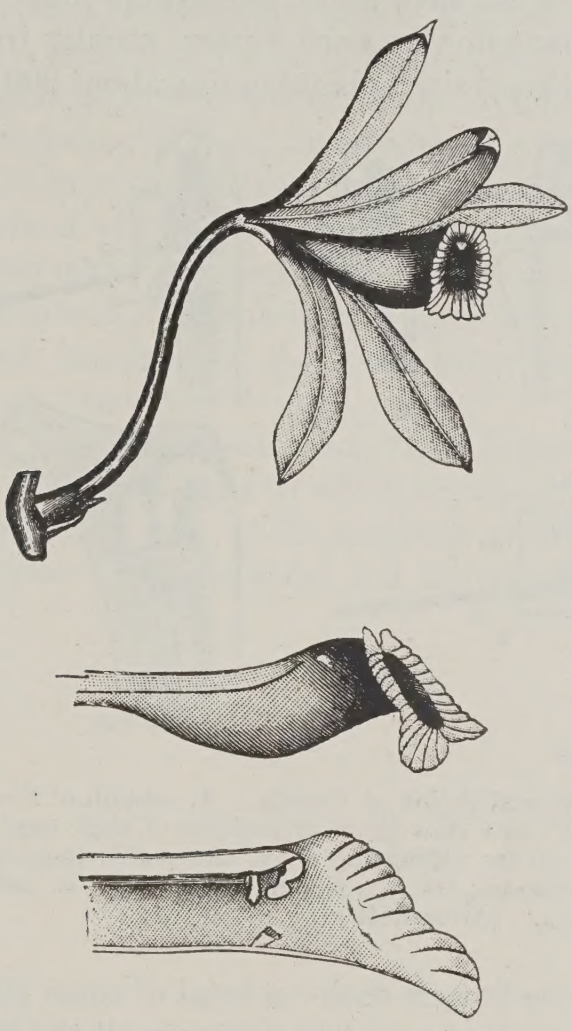


FIG. 658.—Flower and floral organs of *Vanilla planifolia*. Above, flower half life size; middle, lip; liddle, lip; below, lip in section. (After Ridley.)

flowered but set no fruit. Evidently this was due to the lack of the proper insect to effect pollination. Professor Morren, of the University of Liège, was the first to demonstrate that vanilla could be cultivated in tropical countries and a crop secured if hand pollination was resorted to. One of the problems has been to secure a suitable tree to serve as a support, and many planters

have resorted to the use of wooden posts with wooden bars extending from one to the other at the top. The plant is propagated exclusively by cuttings.

In its native country, pollination is accomplished by bees of the genus *Melipona;* humming-birds are also said to transfer the pollen. No other genus of bees appears to visit the flowers, and hence, outside of Mexico, all of the flowers must be hand pollinated. The plant flowers once a year, usually from September to November, a good sized plant bearing about 200 flower clusters

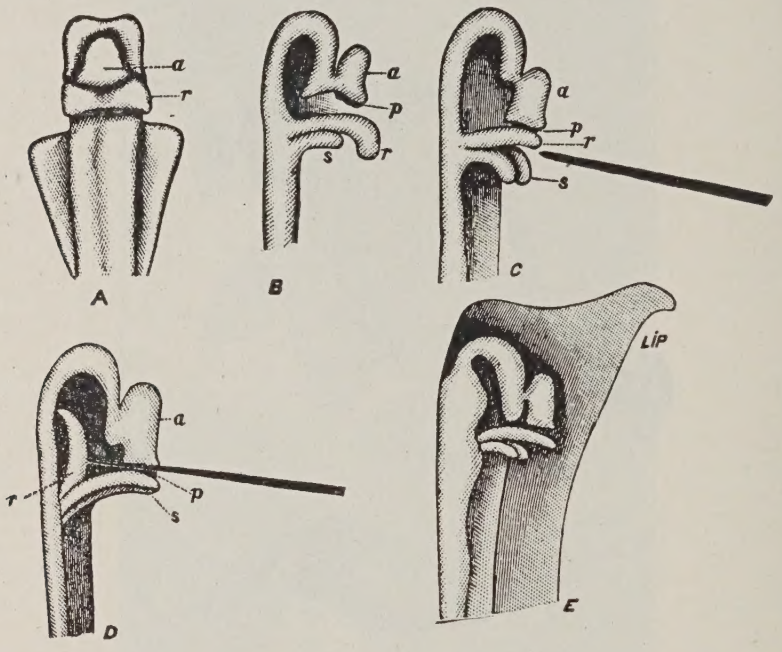


FIG. 659.—Hand pollination of *Vanilla*. *A*, column of flower, front view; *B*, same, side view; *C*, side view showing position of stick used in pollinating; *D*, rostellum pushed up by pollinating stick, and pollen touching stigma; *E*, side view of column showing its attachment to the lip. *a*, anther; *p*, pollen; *r*, rostellum; *s*, stigma. (After Ridley.)

of 15–30 or more flowers each—a total of some 4000 flowers. It is the custom, however, not to pollinate all the flowers—usually only about ten to a cluster. Commonly a given portion (*e.g.*, one fourth) of a plantation is fertilized only once in four years; this practice avoids weakening the plants too greatly.

The flowers remain open only one day and pollination must proceed promptly and rapidly. Women and children are largely employed for this purpose, and a skilful worker can pollinate from 1500 to 2000 or 3000 a day (7 a.m.–3 p.m., when the flowers begin to close). The workers carry a number of splinters of

bamboo or wood about the size of a toothpick. Holding the flower in the left hand they lift the anther cap and the rostellum which covers the stigma (Fig. 659). The pollen-masses are removed with the end of the splinter and placed on the stigma under the rostellum. When the rostellum is released it returns to its original position and presses the pollen against the stigma. In nature, of course, cross-pollination is the rule, and this would probably give a somewhat better quality of fruit, but in practice this would require more time and labor and would not pay.

The pods are picked when green and must be cured before they are marketable; in curing they become almost black, and the oil (called "Balsam of vanilla") gradually increases in quantity, due probably to enzymatic processes taking place in the tissue of the pod. About a month is required for the pods to fully ripen.

The constant handling of the vines often causes a form of illness known as "vanillism."

An artificial vanilla may be made from *Eugenol*, a substance derived from oil of cloves and to which the characteristic odor of that oil is due (*Cf.* p. 694). The artificial product, however, is said to be inferior to the genuine, and the vanilla industry still flourishes.

PART V
GENETICS AND EVOLUTION

CHAPTER XL

HEREDITY, VARIATION AND ENVIRONMENT[1]

Introduction.—The three words, heredity, variation, and environment, when accurately understood, practically express everything associated with an individual's life, be that individual plant or animal (including man). It seems, therefore, best and most logical to treat them together so that students may understand their close relationship and form a true picture of their comparative importance. For in the minds of many, environment and heredity have often been regarded as two opposing forces, each fighting to obtain a preeminence in the individual organism's makeup. The controversy, however, wages as to the effect of different environments on the same hereditary constitution and not between the importance of heredity and environment.

As demonstrated in other chapters, all organisms are described in terms of characters. These are the ordinary descriptive units used to distinguish one individual from another, one variety from another, one species from another. It is of primary importance then to understand what the student of biology fundamentally means by a character. Flower color is a good example. Although some of the varieties of peas (*Pisum* sp.) possess a heredity substance which is passed on from generation to generation through both egg and sperm and which under most environmental conditions in which peas will grow and flower, will produce pink flowers, yet under certain environments such as warm, rainy, cloudy weather, the flowers of these varieties will be white instead of the expected pink. Varieties of lettuce which are grown for market as head lettuce require a specific type of environment (cool, moist weather) to have this character. If grown in hot weather, they usually send up a flowering stalk and eliminate the head phase. Cabbage of many types in some tropical regions

[1] Chapters XL–XLII are by Dr. Orland E. White.

does not produce heads, although the hereditary part of the character is not lacking. Perhaps one of the most striking cases to illustrate this point is the Chinese primrose. Baur found that the red primrose (*Primula sinensis rubra*) when grown under moisture and shade conditions at a temperature of 30°–35° C. had white flowers, while the same plants grown at 15°–20° C. were red-flowered. By changing from one environment to the other during the blooming period, a single plant of this variety was made to show flowers of both colors. Characters then are the result of the interaction of both heredity and environment. The expression of any organism's inheritance takes place in the presence of an environment of some kind, and while in general the inheritance is the most important, because it cannot be altered when once determined, who shall say that finding the most ideal or favorable environment in which a particular inheritance can express itself is not also of equal importance? Discussions involving such questions as "which is the most important—environment or heredity?"—are, as a rule, arid wastes of time, although in specific cases they may be of the utmost importance.

Heredity.—Heredity expresses the relation between parent and offspring, with reference to what the offspring receives from its parents at the moment of fertilization. Through the egg and sperm, two minute bits of matter invisible to the unaided eye, all the complicated design of the most intricate organisms is transmitted, be it either a California big tree, an elephant or a human being. But in the fertilized egg there are few visible differentiating features, so few that those who classify organisms would not care to undertake to determine the species or even the genus at this stage. The individual life of a plant or animal really begins with the undivided fertilized egg. From then on environment begins to play its part in molding characters. All that the organism, plant or animal, has to start with is its inheritance. When two plants are alike in certain characters, especially when they are within the same species, we ordinarily say this is because of their similar inheritance. This fact is supposed to establish a genetic or genealogical relationship, and in many cases it does, but as we shall see later, there are numerous exceptions. The aphorism that "like begets like" is true only in a general way or in very special circumstances. If you doubt the

truth of this statement, experiment yourself with ordinary field corn, or the seeds of various fruit trees, such as plums, cherries, oranges and dates. Compare the children and parents among your acquaintances and friends. Under ordinary conditions, within the same species, like rarely begets like. Part of the plant and animal breeder's work is to bring about these special conditions so that parent and offspring, at least as regards their essential characters, are alike. This is what is meant when we speak of a variety or race as breeding true.

Variation.—"The organic world as a whole is a perpetual flux of changing types" writes Francis Galton, one of the pioneers in the scientific study of variation, heredity and environment. "Nothing is constant, but change" writes a well known philosopher. Without doubt the most striking fact about the world we live in is its infinite, endless variety. New types of plant and animal life are constantly arising now, as well as in the past, either from old forms or combinations of old forms. The old pollard tree of evolution is still sprouting vigorously. These new forms are to be seen in the gardens as vegetable, fruit, or floral novelties, or at the flower shows as new carnations, chrysanthemums, roses, and orchids. They are to be seen in the plant breeders' experimental plots, at the trial grounds of the great seed houses, or even occasionally in wild nature. And as human beings we see only the most obvious variations. For did we know corn as well as we know our own kind, every plant would stand out as in human beings, a distinct and distinguishable unit, a corn personality or "cornality."

The differences between plants, particularly between parent and progeny, we call *variations*, irrespective of how these differences are brought about. Variation occurs in all conceivable directions, as to color and form of flowers and fruit, in height, in number of leaves per plant, in number, arrangement, and symmetry of flower parts, in the shapes of stems, in the length of life, in the ability to resist or succumb to diseases, in the high or low oil, protein, starch, rubber content, etc. Variation occurs among the leaves of the same tree as in the mulberry (Fig. 661) and sassafras, and among pods on the same pea plant, although variation in such cases does not often reach the extreme diversity that it may from the progeny of the same plant. Among the California

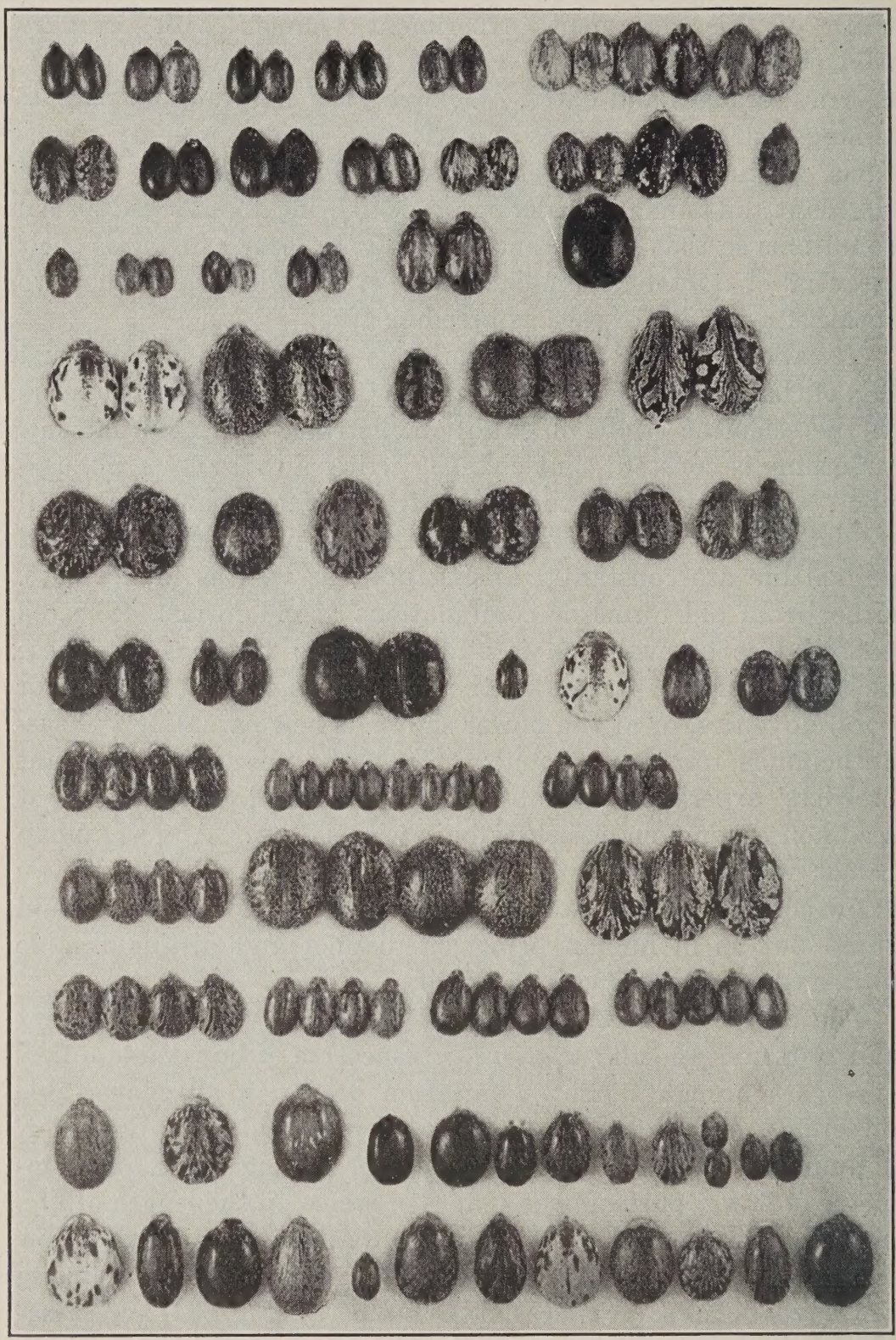


FIG. 660.—Seeds of different varieties of the castor oil bean, (*Ricinus communis*) showing the great variation in size, pattern, color, and shape that has taken place within a single species, the only representative of its genus. All these types cross freely and their hybrids are fertile.

navel oranges (Washington navel) there are many differences—in size, in thickness of peel, in amount of juice, in yield, and in sugar content—yet these oranges are all fruits of what is essentially one tree that has been propagated by budding. Over 1600 varieties of pears have been grown in the United States, and these varieties have all originated through variation from two or, at most, three original species. Still more striking are the number of apple varieties, over 2000, which have been under cultivation in this country, and these, too, have come for the most part

FIG. 661.—Variation in mulberry (*Morus alba*) leaves from the same tree.

from two original wild species. All the numerous types of cabbages, viz. cauliflower, brussels sprouts, collards, red, Savoy and green head, broccoli and kholrabi, are believed to have originated from the wild headless cabbage of the cliffs of southern and western Europe (see Fig. 422, p. 607). Lettuce, too, has varied so greatly since the first primitive tribesman saw in it an inviting vegetable, that today we would hardly recognize the wild, weedy ancestor over which we often tramp in vacant lots as the progenitor of our cooling salad. (Figs. 662, 663.) And so one

might go on indefinitely through the whole list of plants that have come under cultivation and uncover the same story.

The rate of variation in plants apparently is not always the same. The lily-of-the-valley and asparagus on the one hand have but few varieties, while the other extreme is represented by the chrysanthemum, the varieties of which number thousands. Yet all three of these plants have been propagated by millions over a long period of time and in very diverse geographic as well as physical environments. Many of these new forms—these variations—would be given the rank of species were they found

FIG. 662.—Rosette of the common waste-land weed, *Lactuca scariola* or "wild lettuce," the supposed ancestor of all the cultivated lettuces. Compare with figure 663.

under natural conditions. For variation, as a great mass of observations show, follows the same laws and proceeds in the same fundamental manner in nature where man for the most part is unable to look on, as it does in cultivated plants where it is much to his advantage to keep account of them.

Methods of Studying Variations.—Variations are scientifically studied by two different methods—statistical (biometrical) and experimental, though the latter method involves also the use of many principles of the former.

The Statistical Method.—Studying variation by purely statistical methods was more in vogue a decade ago than now. At

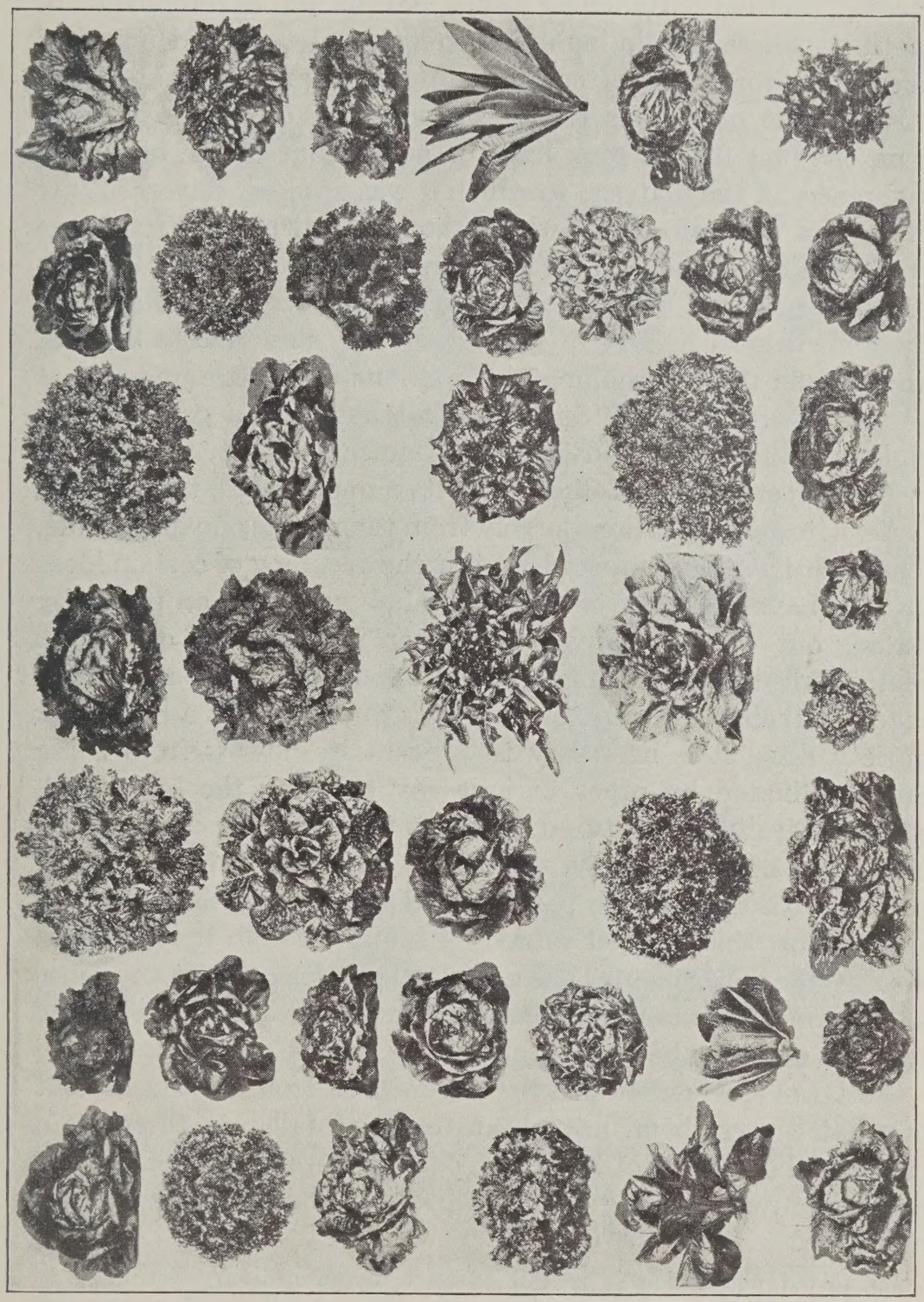


FIG. 663.—Typical rosette plants of forty two different varieties of lettuce. (Modified from W. W. Tracy, U. S. Dept. Agric.)

the present time, its best features are incorporated in the experimental method. Its chief value lies in its development of methods where results involving small numbers can be checked accurately for error, after all ordinary precautions have been taken. The objections to the statistical method arose largely from the fact that it took little or no account of the biological differences of the material to which it was applied, thus resulting in certain generalizations which though statistically true, were not biologically true. Large numbers of individuals were studied, but this material usually consisted of a "mixed population,"[1] the geneological history of which was only imperfectly if at all known, and the environmental conditions were little understood or were disregarded. "Statistical methods are a great aid to biologists, but only an aid" says the Danish biologist, Johannsen.

The Experimental Method.—As its name implies, this method derives its generalizations largely from the results of experiments. The experimentalist proceeds to test the accuracy of certain ideas he may have secured from his general observations on plants by finding out what actually does happen in any given case. Do plums breed true? Some varieties do breed true as regards many of their characters, but in order to prove that a particular variety does, it is necessary to prevent its flowers from being cross-pollinated by other varieties by covering the buds, and, after the fruits are matured, to plant the seed and compare the characters of the progeny, when they have reached the fruiting period, with those of the parent. This is a very simple illustration of how this method works. Usually, though by no means always, the experimenter has a fairly clear idea of what he wishes to find out before proceeding, and not infrequently what he thought ought to be true turns out the reverse.

Variations, when studied by this method from the standpoint of what causes them, have been found to fall into three main classes—those brought about by changes in environment, those resulting from crossing or hybridization and those caused by mutation.

[1] A mixed population is well illustrated by an ordinary cornfield, as there are usually many types present, many of which might through selection be made to breed true. These types cross or interbreed with each other, so that the progeny of a single plant might have representatives of many of these types.

Variation Due to Environment.—When a number of slips of a geranium plant are made, some of which you keep yourself, and others of which you give to your friends, you will probably observe rather striking differences in them as they grow up—differences in habit, height, number of flowers, amount and character of the foliage, etc. These differences or variations are not, however, except in very rare cases, due to any change or alteration in their hereditary substance, but solely to differences of one kind or another in the environment under which they grew from slips. Common environmental distinctions of this type may be due to differences in soil, temperature, light, and moisture. A striking illustration of the part such factors play in character expression is exemplified by the experiments of Klebs on the common houseleek, "hen and chickens" (*Sempervivum*). All the plants in the illustration (Fig. 664) were grown from slips or

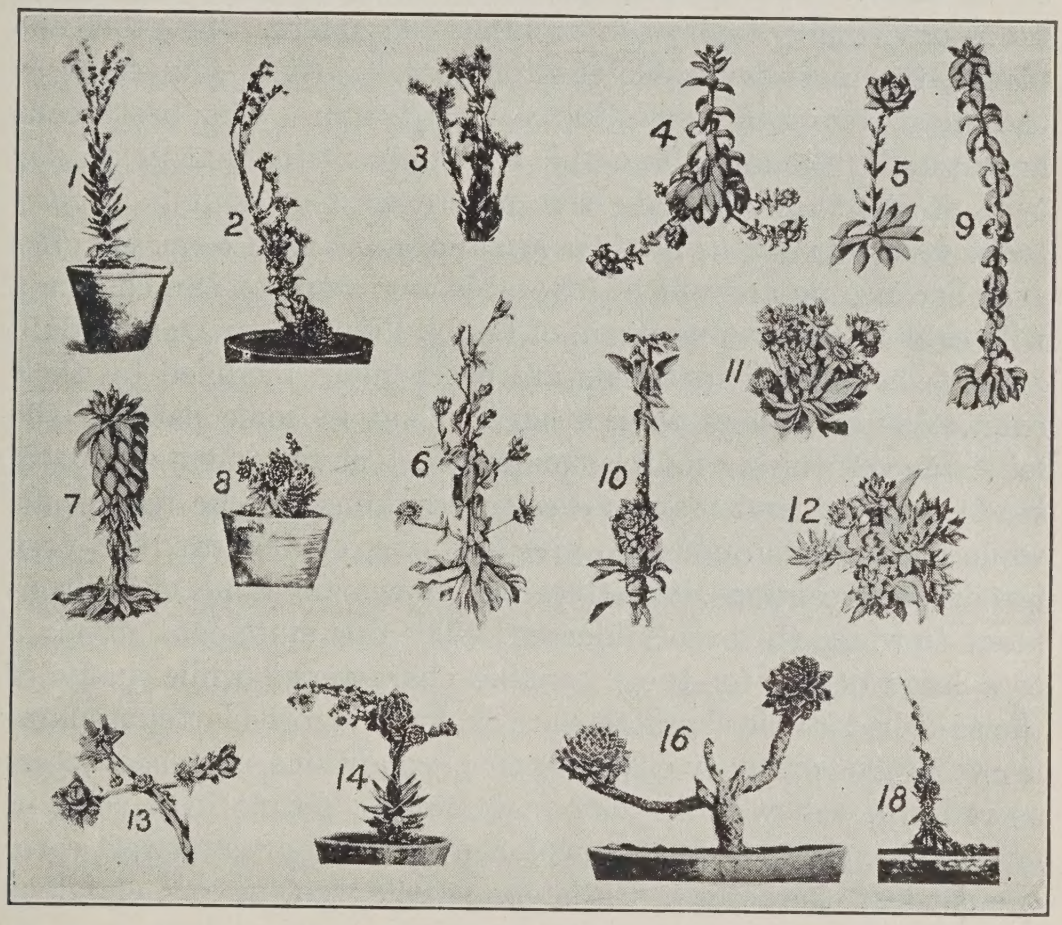


Fig. 664.—Illustrations of the effect of different environments on the house-leek (*Sempervivum*). (Modified from Lotsy after Klebs.)

cuttings from one plant. Hence all possess the same hereditary make-up, but when subjected to different environments, such as noted above, they grew up strikingly distinct, though there is no difficulty in recognizing them all as forms of the same species. Each type is capable of producing all the other types when subjected to the appropriate environment. Slips or cuttings from each of them grown under exactly the same environment would all be alike. This illustration amply demonstrates the importance environment plays in molding characters. To grow fine plants, the most favorable environment is just as important as the most favorable hereditary constitution. The best seeds grown under the most favorable environment for that particular type of plant always bring the most desirable results. *Neither factor must be neglected, but the hereditary one must be looked after first,* because no amount of favorable environment can change a wild cabbage into a fine strain of Dutch Flathead or Danish Ball.

Some hereditary materials are much more modified by their external environment than others. That is, some parts of the inheritance furnish a foundation on which environments of many kinds may act and many different reactions will be the result, while other parts appear to give but one, or at most, but very few distinct reactions, it matters little how many kinds of environment to which they are subjected. The first statement accounts to a large degree for the "variable characters," while many of the so-called stable characters are explained on the latter assumption. Under ordinary environmental conditions, such characters as red and yellow fruit color in tomatoes, purple fruit color in eggplants, yellow endosperm color in Golden Bantam sweet corn, the cut-leaf character in *Chelidonium*, the weeping or pendulous character of many ornamental trees, are only slightly if at all modified by environmental changes. Other characters, examples of which are susceptibility to various diseases, height, stooling of cereals, length of time between germination and fruiting, and size and yield of fruit, when contrasted with the first, are often strikingly influenced by environmental changes ordinarily encountered. The first group of characters are representative of those hereditary expressions that enable us to make a somewhat stable classification of plants. They allow us to predict with great certainty that tomato seeds will always produce tomato

plants and not eggplants (despite any changes in environment). Peaches give rise to peaches anywhere in the world where peaches will grow. No environment we know of will change them to nectarines (smooth-skinned peaches) or to apricots.

Acquired Characters.—Much of the discussion concerning the inheritance of acquired characters has been profitless because of a lack of clear definitions or concepts. What do we mean by acquired characters in terms of modern biology?

An acquired character has been defined as "a modification of bodily structure or habit which is impressed on the organism in the course of the individual life." Illustrations of such characters are dwarfing of plants due to poor soil or drouth; changing of flower color by the use of certain chemicals or soils as is done with the pink hydrangea, thus changing it to a blue flowered form; increase of fruit and flower size by thinning or dis-budding, together with rich soil. Plants in which the usual characters have been thus modified produce seed from which progeny grow that do not reproduce these modified characters except when the same environments are again imposed upon them. If these "acquired characters" or modifications were shown to be inherited, as this expression is commonly understood, the progeny of such individuals would reproduce the acquired characters largely irrespective of whether the environment was the one under which they were originally produced or not. The experimental work dealing with this question, while not conclusive, is largely negative, and for all practical purposes, "acquired characters" may be regarded as non-inherited.

Running Out of Varieties.—There is a widespread, perhaps age-old belief among growers of certain types of crops, that varieties eventually "run out," *i.e.*, lose the characters that originally made them so desirable to grow. There are two classes of these crops, those propagated from seeds and those grown by vegetative methods, such as slipping, budding, and grafting. The first group is represented by sugar beets, various garden vegetables and flowers, cereals, and flax. The probable explanation of their loss of popularity involves several factors, some of which are due to heredity. The chief environmental factors are the changes in environment to which they are subjected due to their removal from the environment in which they first originated

and attained their popularity. These changes may take the character of new or little known diseases, changes in the character of the soil, changes in the light relations (length of day, intensity of light, etc.) and changes in moisture conditions. As our knowledge of the relation of environment to different types and varieties of plants grows more detailed, definite, and accurate, this idea of the running out of varieties as a wide generalization disappears. The phase of this question that involves heredity necessitates a detailed knowledge of genetics, and cannot be considered here except in the most general terms. Suffice it to state that many varieties are not sufficiently "purified" before they are distributed, hence they contain a fair percentage of rogues (off-types) which often seed more freely than the desirable type, and unless destroyed ruthlessly, soon largely supplant it. Crossing also takes place between the desirable and the rogue types. Undesirable mutations may arise occasionally. Thus the situation becomes more and more complicated.

The second group, or asexually propagated crops, run out or cease in part to have their original desirable characters also from both environmental and hereditary causes, each of which, in practical plant breeding, necessitates different control measures. Crops of this type are represented by most of the tree and bush fruits, many ornamental herbaceous perennials (hollyhocks, iris, peonies), bulbous plants (lilies, gladiolus), field and truck crops (potatoes, sweet potatoes, pineapples, sugar-cane, strawberries, and asparagus). The environmental troubles affecting the first group are also undoubtedly factors responsible for the belief that varieties run out in this group, but there is the additional factor here of the diseases being carried along continuously with their hosts, and becoming more and more firmly intrenched in a cumulative fashion. This has led to the propagation of relatively disease-free "seed," for example, in some potato growing regions, in which case diseased plants are rogued or eliminated before the crop is gathered. Many named varieties of ornamental plants (hollyhocks, verbenas, delphiniums) which were once propagated asexually are now grown from seed because of this disease problem. Bud sporting has also been a factor leading to deterioration in some crops (grapefruit, oranges and sugar-cane). Propagation of these crops is accomplished in such a wholesale

manner that non-desirable variations would pass unrecognized. Recently the citrus growers have been made to realize the importance of using buds only from trees of recognized merit, as evidenced by their performance. This at least eliminates the danger of planting whole groves of undesirable trees resulting from bud sports, such as the sport of Marsh Seedless grapefruit, which has fruit full of seeds. The point in discussing this problem here is to show that running out is due to a variety of causes, both environmental and hereditary, and not to an inherent trouble (degeneracy, senility) due primarily to asexual propagation, inbreeding, and the absence of cross-fertilization. In a report on 67 varieties of potatoes tested in Sweden by Heribert-Nilsson and cited by Hayes and Garber,[1] the variety "Hvit Jämtlandspotatis," although cultivated for over 100 years, outyielded all others. Numerous other examples of this kind could be cited.

Variation Due to Crossing.—The progency of crosses are called *hybrids*, and the process, *hybridization*. For a century or more gardeners and others interested in plants have known that crossing two different types of plants, *i.e.*, two varieties of one species or two closely related species, often resulted in progeny with hitherto unknown characters. It was also known that in at least some cases the progeny might be very variable. Knowledge, however, in this field was, until comparatively recently, in an extremely chaotic state. This was still the "dark age" when much nonsense and superstition passed as science. Men were still groping almost blindly for clews and light, and the light obtained for a time only led to greater confusion and wilder generalizations. To paraphrase a great writer of the time, this whole subject was a maze in which science lost itself. Experimental inquiry, not speculation and data based on casual observations, was the great need. Darwin, Naudin, and Francis Galton made some headway towards orderly arrangement of the known facts regarding crossing and variation, but it was not until 1900 that the mists and fogs of centuries lifted and the maze began to be intelligible. In this closing year of the 19th century three European botanists—de Vries, Correns, and Tschermak, unknown to each other, while conducting experimen-

[1] Hayes, H. K., and R. J. Garber. Breeding crop plants. p. 232.

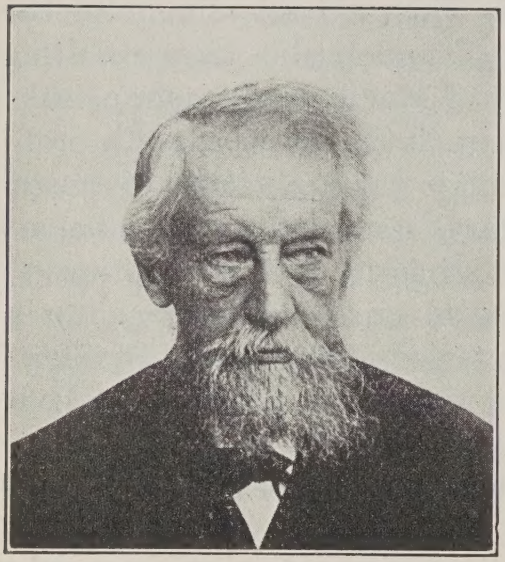


FIG. 665.—Hugo de Vries.

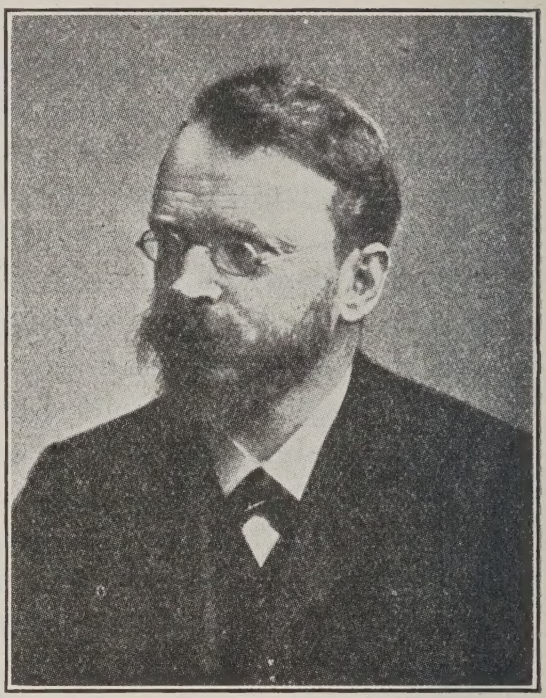


FIG. 666.—Carl E. Correns. (From Zeitschrift für Pflanzenzüchtung.)

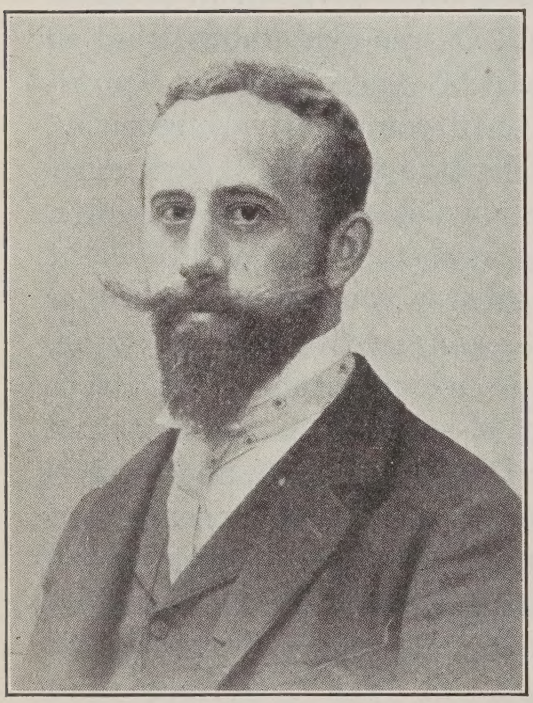


FIG. 667.—Erich von Tschermak. (From Rpt. 3rd Internat. Conf. on Genetics.)

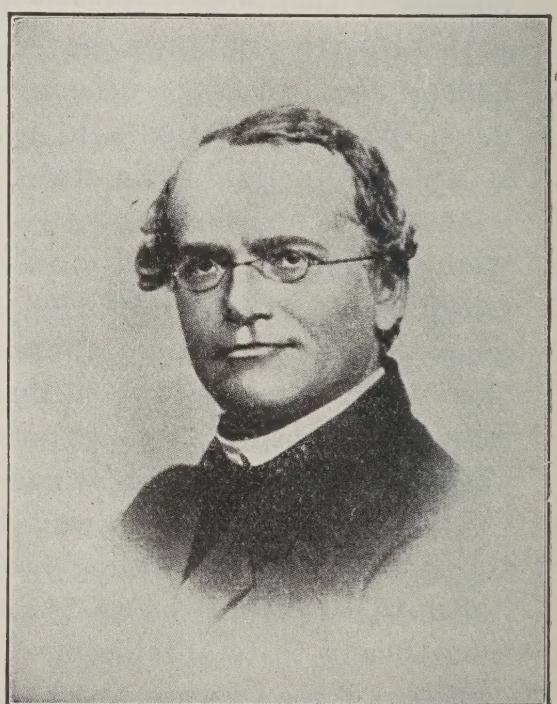


FIG 668.—Gregor Johann Mendel, at the age of 40.

tal researches on plants, rediscovered, almost simultaneously, what are now known as Mendel's laws.

Mendel.—Gregor Johann Mendel, (1822–1884) was an Augustinian monk, who had studied science at the University of Vienna and later taught in the *Realschule* at Brünn, Austria (now Czechoslovakia), where he was a member of the Königskloster or Augustinian monastery, and of which he afterwards became abbot. He was especially well trained in physics and mathematics and had been brought up in a farming community where he was early initiated into the mysteries of agriculture and fruit growing, and no doubt had the thorough training in economic botany that is every farm boy's heritage the world over. Perhaps it was this training, associated with a brilliant, analytical, inquiring mind, that led him to devote eight years to experiments on peas in the Königskloster garden in an effort to find the fundamental clew, the Rosetta stone, that would show us how to unravel the tangled skein of our heredity, that would allow us to arrive at somewhat stable generalizations.

Mendel's Experiments.—The experiments were carried out in the garden of the Königskloster just previous to and during our Civil War period. The now famous paper[1] involving the results obtained and the conclusions reached, was read before the somewhat obscure scientific society of Brünn in 1865 and published in 1866, but it remained all but unnoticed until similar results as mentioned above, were discovered in 1900.

Darwin's epoch making work, "The Origin of Species," was published in 1859, but Darwin apparently never came in contact with Mendel's paper or work, although it has been stated that Mendel embarked on his experiments because he did not find himself in entire agreement with the views of Darwin, which were then attracting much attention. Mendel appears then to have started his work on peas primarilly because of his interest in the manner in which new species originate, this being the dominating and most puzzling biological subject of the time. Through

[1] Mendel, Gregor Johann. Versuche über Pflanzen-Hybriden. (Experiments in plant hybridisation.) Verh. naturf. Ver. in Brünn **4,** Abhandl., p. 3–47. 1865 (1866). Reprinted first in Flora, 1901. English translation in Jour. Roy. Hort. Soc. **26:** 1901. Also reprinted in Mendel's Principles of Heredity by W. Bateson and in Genetics and Eugenics by W. E. Castle.

his studies on hybrids, he undoubtedly thought, as did the hybridizers before and after him, to obtain much light on this subject. Varieties of peas were used in these experiments, not because of any interest Mendel had in peas as peas, but in peas as the best material he could find through which to test his ideas and obtain new light on the problems of inheritance and variation. Mendel's paper is a classic, both because of its content of fact and its clear exposition of how he set about his work. Hence, for

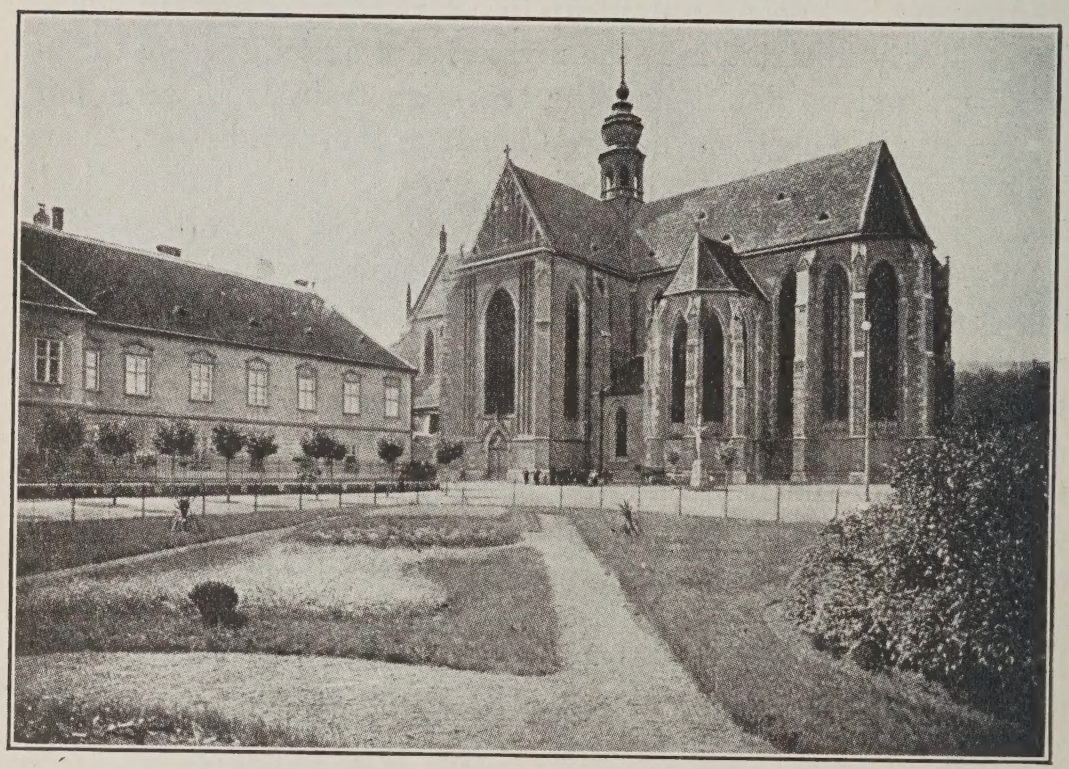


FIG. 669.—Augustinian cloister at Brünn with the chapel. On the left the abbot's lodgings where Mendel lived. (From Rpt. 3rd Internat. Conf. on Genetics.)

these reasons and because it is a model scientific paper, it should be read by all students interested in biology.

Mendel set himself the problem of determining how the characters of hybrids were inherited and to find the laws such inheritance followed. This involved seeing that the varieties first bred true for a number of generations to the characters he wished to study, the determination of the number of forms in which the hybrid offspring appeared, and their statistical relations to each other in each generation. Mendel realized that in

peas he had found a material very suitable for his experiments in terms of what he regarded as prerequisites. The material necessarily must possess clearly *differentiating characters, be easily protected from cross-pollination, suffer no marked disturbances in its fertility, be easily grown, and have a short maturity period.*

The Chosen Seven Pairs.—The pairs of constant differentiating characters studied in peas were round (smooth) vs. wrinkled

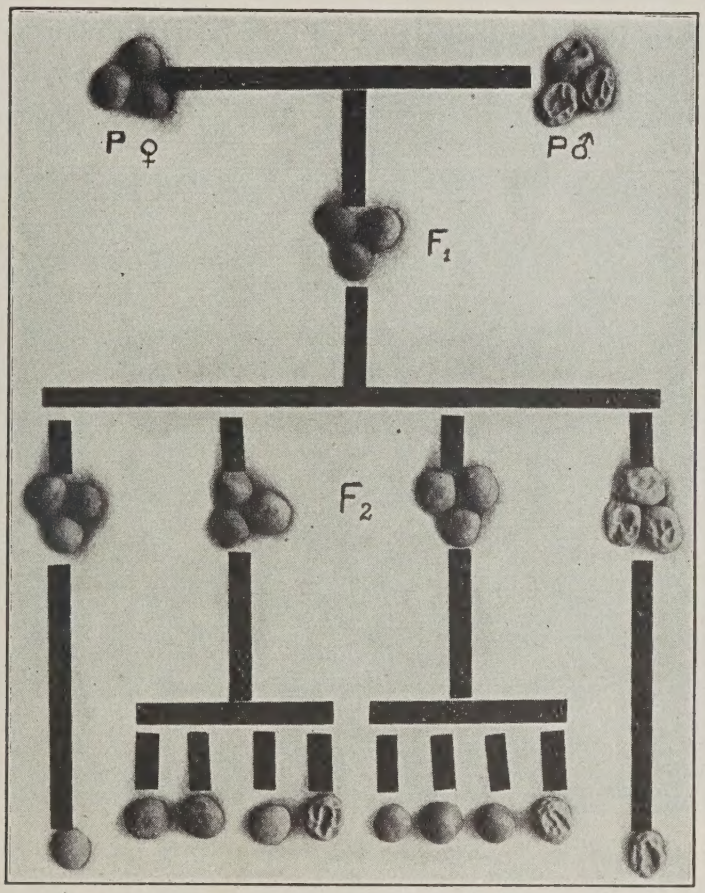


FIG. 670.—Diagram illustrating the results obtained from crossing a variety of garden pea breeding true to smooth cotyledons with one breeding true to wrinkled cotyledons. One of the chosen 7 pairs.

(angular) cotyledons; yellow vs. green cotyledons; color vs. colorless (white) seed coats and flowers; parchmented (smooth, inflated with a parchmented tough lining) vs. non-parchmented (constricted, without parchment lining, and edible as are string beans) pods; green vs. bright canary yellow unripe pods; normal round stems with axillary flowers vs. fasciated (flat, ribbon-like) stems with terminal or umbellate flowers; and tall (6 to 7 feet) or

dwarf (¾ to 1½ feet) stems. The members of such pairs are known as *allelomorphs* and each member is said to be *allelomorphic* to the other.

Experimental Results Involving a Single Pair.—When a variety of pea breeding true to green (G) unripe pods was crossed reciprocally (G × Y, or Y × G) with a variety breeding true to yellow (Y) unripe pods, the *first hybrid* (F_1 *or first filial*) generation all had green pods, irrespective of the number of plants involved (one, one hundred or one thousand) or the way in which the cross was made. When seed obtained by self-pollinating any one of these (F_1) plants was gathered, planted, and the characters of these

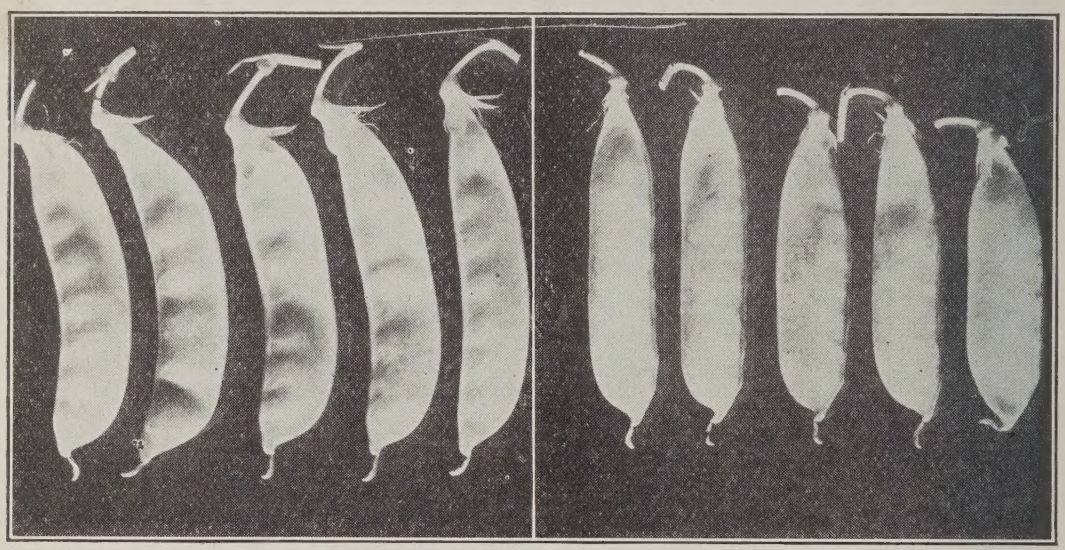


FIG. 671.—Non-parchmented, edible, constricted pods (left); and parchmented, inedible, non-constricted pods (right). Another pair of pea characters studied by Mendel.

second hybrid (F_2) generation plants were observed, approximately one fourth had yellow pods, thus giving a proportion of 3 green pod plants to 1 yellow pod plant. Each and every F_1 plant tested was found to give the same kind of progeny in approximately the same proportions. With seed obtained from self-pollinated F_2 plants, an F_3 generation was grown. All the F_2 yellow pod plants tested gave only yellow pod progeny in F_3, while approximately only one out of every three of the F_2 green pod plants bred true in F_3. The remaining two thirds had progeny similar in number of kinds (classes) and in ratio to that obtained from growing seed from F_1 plants. Diagrammatically presented the results were:

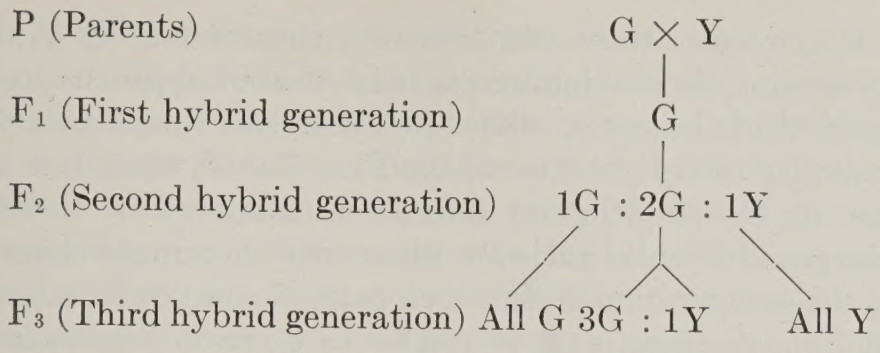
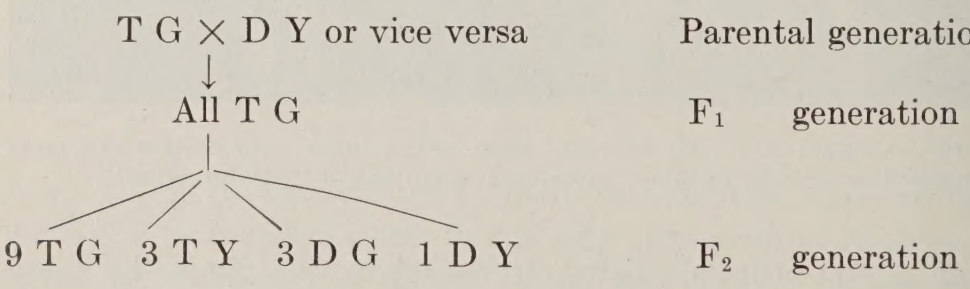


FIG. 672.—Flowers and pods axillary, stem round (left); and flowers and pods umbellate or in a terminal "bouquet," stem flat or fasciated (right).

Each of the other six pairs of characters was given the same experimental treatment with similar results as to the character of the F_1 generation, the number of kinds and the ratio of individuals of each in the F_2 generations and as to the character of the F_3 progeny. In each case, one character appeared to the exclusion of the other in F_1. The character that appeared was called *dominant,* while the character that was not present was called *recessive.* In the F_2 generation in each of the seven experiments, the plants with the dominant character were approximately three

times as numerous as those with recessive characters. In F_3, in each experiment, the F_2 dominants bred true in approximately only one-third of the cases, while the other two thirds gave F_3 progeny similar to the progeny of the F_1. The F_2 recessives all bred true in F_3, showing no indication whatever of having had as one grandparental ancestor, plants with dominant characters. In the enumeration of the seven pairs of characters studied by Mendel, the dominants are placed first, *e.g.*, round (dominant) vs. wrinkled (recessive) cotyledons.

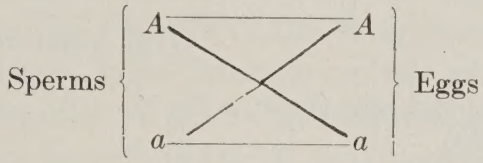
Experimental Results Involving Two Pairs.—When Mendel crossed varieties of peas differing in two pairs of characters, such as a tall plant having green pods with a dwarf plant bearing yellow pods, the F_1 generation results were those expected where dominance is complete, *i.e.*, all the F_1 plants were tall and had green pods. The F_2 progeny of these tall green podded plants consisted of four classes or kinds repeatedly approximating a ratio of 9 tall green pod: 3 tall yellow pod: 3 dwarf green pod: 1 dwarf yellow pod. The details of their F_3 progeny are too complicated and long for discussion here. It is sufficient to indicate that they expressed themselves in definite mathematical proportions which were shown by repeated experiment to be predictable and to give always essentially the same results. Diagrammatically the F_1 and F_2 results would appear thus:



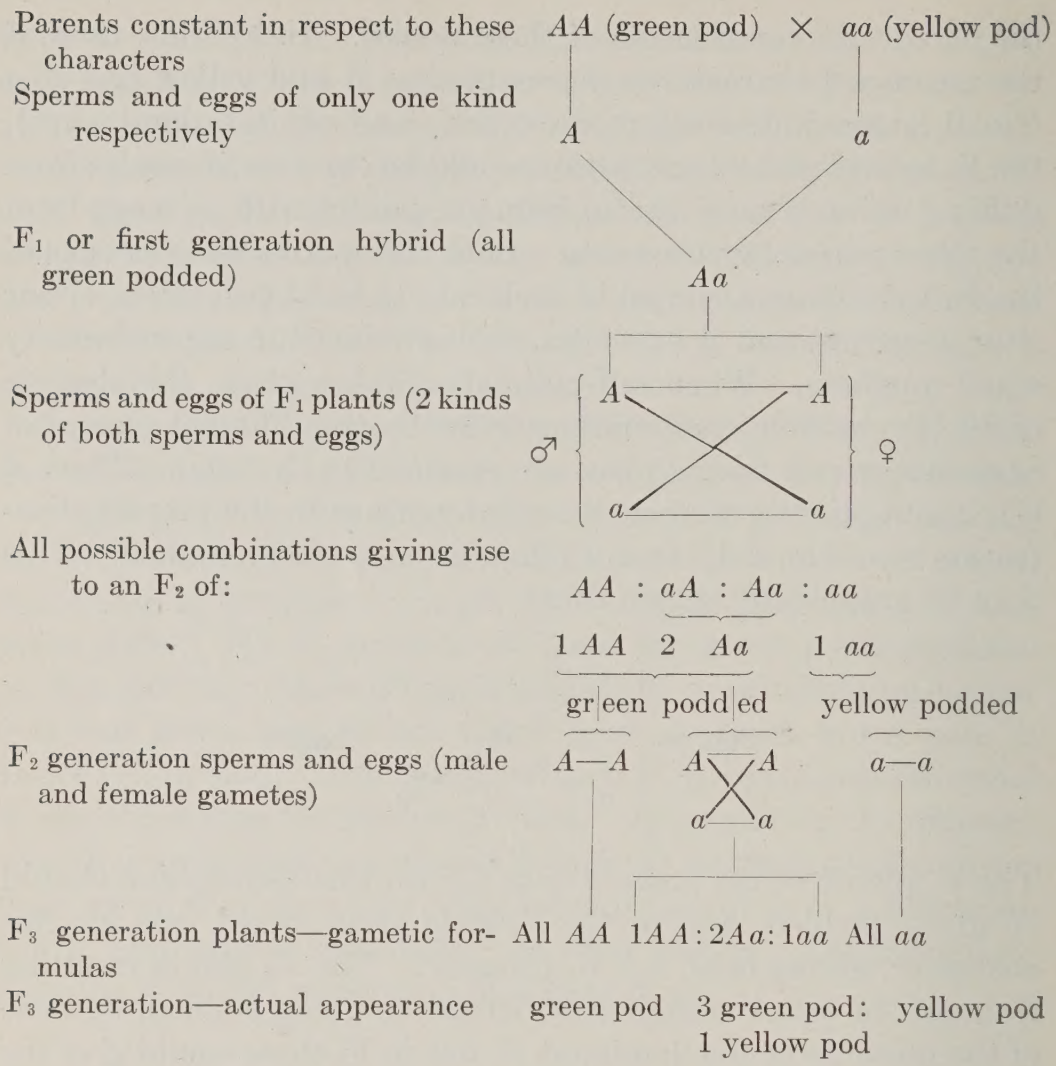
In the accounts of both the preceding experiments, only facts have been cited. No theories or hypotheses have as yet been presented.

Mendel's Explanation.—Mendel interpreted his results by assuming that the germ cells, *i.e.* the male (sperms) and female (eggs) gametes of peas, differed from each other in respect to the characters they carried, each character being represented *once* in

the hereditary constitution of these bodies. In hybrids, then, if the green pod character is represented as *A* and yellow pod as *a* (small letters indicating recessiveness, and capitals dominance), the F_1 hybrid plant constitution would be *Aa* since it results from either a union of an *A* sperm from one parent with an *a* egg from the other parent or vice versa. Both the sperms and the eggs of the F_1 hybrid are assumed in each case to be of two kinds, either *A* or *a* sperms, and *A* or *a* eggs, each produced in approximately equal numbers. When self-pollination takes place, the chances of all the possible combinations between the different classes of eggs and sperms taking place are assumed to be equal. Thus, if this assumption is correct, the combinations in the present illustration would be *AA*, *Aa*, *aA* (these two are alike), and *aa*. This may be graphically shown thus:



The F_2 plants of the composition *AA* on this assumption should be green podded, and in the F_3 generation, breed true for this character, giving only *AA* F_3 progeny. The F_2 plants resulting from an *Aa* or *aA* combination would be green podded, because of the presence of the dominant *A*, but in F_3 these would give the same kinds of progeny and in the same proportions as in the case of the F_1 hybrids, because their composition as respects this pair of characters is the same. On this assumption, the F_2 *Aa* plants then, should have F_3 progeny of two kinds—green podded and yellow podded—in approximately the ratio of 3 green podded: 1 yellow podded. There remains the F_2 *aa* plants which should be yellow podded and breed true in F_3, *i.e.*, have only yellow podded progeny. Diagrammatically these results would be represented thus:



Though this explanation is a hypothesis, the actual results obtained by Mendel and, since his time, by other experimenters, accord perfectly with what is assumed should take place if the hypothesis is true.

The explanation of the second experiment is slightly more complicated, in that one must follow two pairs of characters and their gamete representatives. In this case the F_1 hybrid may be indicated as *AaBb*, *B* and *b* representing respectively the tall and dwarf characters. The gametes (sperms and eggs) of each of these F_1 hybrid plants would be of four kinds instead of two. Use may be made of the checkerboard method (Punnett square) to illustrate them and their possible combinations:

Egg cells or female gametes (eggs)	Male cells or male gametes (sperms) *AB*	*aB*	*Ab*	*ab*
AB	*AB* *AB*	*aB* *AB*	*Ab* *AB*	*ab* *AB*
aB	*AB* *aB*	*aB* *aB*	*Ab* *aB*	*ab* *aB*
Ab	*AB* *Ab*	*aB* *Ab*	*Ab* *Ab*	*ab* *Ab*
ab	*AB* *ab*	*aB* *ab*	*Ab* *ab*	*ab* *ab*

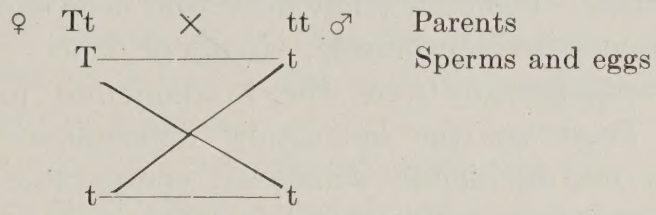
The results in terms of gametic composition would show 9 kinds in the proportions of $1AABB:2AaBB:2AABb:4AaBb:1aaBB:2aaBb:1AAbb:2Aabb:1aabb$, while from the standpoint of what their actual appearance would be when growing the result would show four kinds in the ratio of $9AB$ (tall-green pod) : $3Ab$ (dwarf-green pod) : $3aB$ (tall-yellow pod) : $1ab$ (dwarf-yellow pod). These results can be obtained in another way by multiplying the two simple ratios of $1AA + 2Aa + 1aa$ and $1BB + 2Bb + 1bb$ in the form of algebraic equations. The point in calling attention to the more complicated experiment is that it demonstrates that not only may two character determiners remain associated (as in the F_1 hybrid of the first experiment) and separate, during the formation of the sperms and eggs of the F_1, as uncontaminated, pure and as entire as when they came from their original parents, but also that two of these character determiners belonging to different pairs but associated in the original parent, as was the case with tall and green pod, gave results in the F_2 generation that demonstrated they were independent entities. In other words, tall and green pod gave a numerical F_2 ratio that could only be obtained in most cases, if tall and green pod were inherited independently of each other. The F_2 results might have shown a ratio of 3 tall green pod : 1 dwarf yellow pod, in which case the obvious interpretation would be that they were completely linked or coupled or most probably distinct expressions due to one pair of hereditary determiners.

Mendel's Laws.—These are two, and possibly three in number, if the law of dominance is included.

1. *Law of Dominance.*—When two varieties, races, or strains of organisms differing in a single pair of constant characters in which each breeds true, are crossed, the F_1 generation plants, as respects this pair of characters, are all alike, and *one character is present to the exclusion of the other,* as is illustrated by each of Mendel's crosses involving only one pair. Tall x dwarf gives F_1 hybrids which are all tall. Dominance is not regarded at present in such an important light as it was a decade ago because in the majority of cases studied (involving hundreds of different plants and animals and thousands of characters) dominance is only partial or incomplete. The F_1 condition in such cases may show various grades of intermediacy. Both characters may be partially present. A cross of a white-flowered four-o'clock with a red flowered form, gives an F_1 hybrid that is dilute red. A fasciated (ribbon-stemmed) tobacco variant crossed with its normal (round-stemmed) parent race gives an intermediate F_1 hybrid. In both these cases the F_2 progeny from self pollinated F_1 plants give a 1:2:1 ratio instead of 3:1 because the two F_2 plants, in the ratio, that will not breed true in F_3 are distinguishable and like the F_1, while the other two classes represent the respective grandparents and, like them, will breed true.

2. *Law of Segregation.*—The first experiment described on page 952 illustrates the *law of segregation, showing that when two varieties or breeds of organisms, such as peas, differing in one pair of true-breeding (constant) characters are crossed, they reappear in their entirety in the F_2 generation, provided there has been no essential change in the environmental conditions.* The actual segregation is not a segregation of characters, but of character determiners, now generally referred to as *factors* or *genes,* and this takes place during the processes (reduction or maturation divisions) which result in sperms and eggs. The separation of the members of a pair of factors during the formation of the sperms and eggs, such as the factor for tall and the factor for dwarf, is referred to as *segregation.* Segregation, it should be noted, takes place not only in hybrids, but also in pure-breeding varieties. Tall varieties of peas have two such factors—they are TT—and the pair of T factors segregate just as those of a tall-dwarf hybrid

Tt do. Segregation may also be illustrated by *back-crossing*, that is, by crossing the F_1 hybrid back to either of its parents. An F_1 hybrid of tall x dwarf crossed back to the dwarf parent, instead of giving a 3:1 ratio, gives a ratio of 1 tall: 1 dwarf. The dwarfs breed true, while the talls in this case are all hybrids of tall and dwarf, as the F_1 generation of pure talls x pure dwarfs would be. Graphically the cross would be:



Combinations 1 Tt: 1 tt

3. *Law of Independent Assortment.*—The second experiment described on page 954 illustrates this law. When races differing from each other in two pairs of true-breeding characters are crossed, in the F_2 generation each pair by itself gives a 3:1 or 1:2:1 ratio, and each pair is independent of the other in its inheritance. When only two pairs are involved, the least possible number of individuals necessary to obtain the expected ratio and demonstrate this fact is 4^2 or 16, but if seven pairs were involved the least possible number required would be 4^7 or 16,384 individuals, representing 2187 different forms, of which 128 (2^7) would be visibly distinct (provided dominance is complete). In other words, if the seven pairs of characters with which Mendel experimented are all inherited independently of each other, the lowest possible number of progeny with which all the classes could be obtained would be 16,384, and even then the likelihood of securing the class that would be recessive for seven characters, of which class only one individual would be expected in this number of plants, would be very remote. With twice as many plants, *i.e.*, 32,768, only two such plants would be expected. Taking data on such an F_2 generation would be an enormous task, as there would be 128 columns necessary to classify the 128 *visibly* (*phenotypically* is the technical term) different kinds. To test out the character of the hereditary constitution of these 128 kinds, by growing F_3 progeny from them and classifying the data thus obtained, would be a well-nigh impossible human task because, classified on the

basis of the laws just enumerated, it is assumed that 2187 different F_2 gametic types are present (different because of the F_1 ♀ and ♂ gametes that produced them). These types are called *genotypes.* Hence the classes and the ratio are described as genotypic because each type is differentiated by a specific difference in gene constitution.

Genetic Terms.[1]—Many terms commonly used have already been defined. There are a few more that need explanation before further procedure is profitable. *Genes* or *factors* (these terms are used interchangeably) are the fundamental units of genetic theory. They are the hereditary determiners of characters, playing a role in biology somewhat comparable to that of the atom in chemistry. The total inheritance of an organism, its whole complement of genes or factors, is referred to as its *genotypical* or *factorial* constitution. In the original conception of gene, as defined by the author of the term, Johannsen, genes are not implicated with chromosomes. This latter statement is also true as regards the original concept of factor. Many workers in genetics now, however, definitely associate these concepts with a portion of a chromosome, as described in later pages. On such a basis a gene is the smallest unit in the chromosome capable of varying. Genes or factors are not concepts synonymous with that of "unit character." *Unit characters* are characters such as yellow immature pods in peas, the inheritance of which, when a yellow podded variety of peas is crossed with a green podded race, is governed by a single gene or factor, as shown by the F_2 generation ratio of 3 green pod : 1 yellow pod plant. Most characters are much more complex in their inheritance. Often many factors are concerned in the inheritance of the hereditary part of a single character. (All characters are due to both inheritance and environment.) The term unit-character is passing out of general use.

Letters representing the genes or factors are called *symbols.* Commonly the same letter is used for the members of a pair of factors (*allelomorphs*), the dominants being indicated by capitals, the recessives by small letters. As one progresses further into the mazes of genetics, complications and difficulties arise from

[1] Excellent and fairly complete glossaries of genetics terms are given in "Genetics in relation to agriculture," by Babcock and Clausen; also in "Breeding crop plants," by Hayes and Garber.

such usage, but these bridges need not be crossed in an elementary treatment. The science of genetics is young, workers are many, facts accumulate rapidly, and new concepts or changes in old ones are constantly arising. Hence the language is constantly changing, broadening, and becoming modified. In certain groups of organisms, such as the sweet pea, the vinegar fly (*Drosophila melanogaster*), maize (corn), and the garden and field pea (*Pisum sativum*), attempts have been made to standardize the symbols in relation to their expression, so that the same gene is always represented by the same letter, just as H in chemistry always represents the element hydrogen.

When a race or variety is constant or breeds true for a particular gene, such as that which primarily determines green pod color in peas, it is indicated by two letters, AA, and the variety is referred to as *homozygous* for this gene, and the individual plants are *homozygotes*. If the plant carries genes for both green pod (A) and yellow pod (a) color, indicated by Aa, the plant is a *heterozygote* and *heterozygous* for this pair. As shown by examples in the preceding pages, a plant may be homozygous for one or more pairs and heterozygous for one or more other pairs.

Hybrid, as commonly used in modern genetic literature, applies to all individuals that result from a sexual union, between two individuals differing in one or more factors. Most wild plants and all bisexual animals are probably hybrids in that they are heterozygous for at least one pair of factors, and probably in the majority of cases, for a large number. An organism homozygous in all its factors is an ideal conception. If it occurs at all outside genetic cultures, it is rare. Plants that are naturally self-fertilized (absolutely cleistogamous, *i.e.*, pollinated in the bud) are more likely to be in this state. Varieties of garden peas belong to this class (cross pollination being rare), while the other extreme is represented in general by the orchids, mammals (including human beings), and the great families of wind-pollinated plants, to which belong corn and various trees—pines, palms, maples, oaks. The processes through which hybrids are produced are referred to as *hybridization* or *crossing*. When a plant is pollinated by its own pollen, it is spoken of as *selfed*, and the resulting seed, as *selfed seed*. In selfing plants, we are *inbreeding* them, *i.e.*, breeding them with themselves. The egg

and sperm are referred to collectively as *gametes*, and sometimes as *germ-cells*.

The formula *Aa* also illustrates the use of the terms *phenotypic* and *genotypic* (*gametic*). Phenotypically the plant is green-pod, since green represents the *visible* expression, but genotypically, it is hybrid for both the green pod and yellow pod factors. If the plant is *AA* or *aa*, the phenotypic and genotypic formulas would be the same. Parent and offspring would in the latter case both look alike and breed alike.

Variation Due to Mutation.—The third type of variation is mutation. Mutation may be defined as variation that cannot be accounted for through changes in environment or through crossing. Mutation, as we shall see later, has been of great importance in bringing about changes in plant characters and hence in the evolution of plants, though possibly crossing has been of equal significance, especially in producing plants more suited to the desires of man. The "weeping" character of willows, mulberries, and birches is an excellent common illustration of mutation. Other common examples are white-flowered forms of wild plants which usually have colored flowers, double-flowered plants, plants with symmetrical flowers from such species as the irregular flowered snapdragon, change in color patterns, in height (dwarfs from talls), in being smooth or hairy leaved or fruited (*e.g.*, nectarine and the peach). A mutation often arises in a variety that has bred true in certain characters for many generations, as illustrated by the production of a ribbon stem (fasciation) plant from the normal, round stem, Cuban variety of tobacco. Among millions of plants of this variety grown in Cuba and elsewhere, this is the only variation known of this type, and this occurred first as a single plant from which thousands of plants possessing this same character have been derived. Associated with its flat stem were other profound differences, such as an increase in the number of leaves per plant, and in flower parts per flower. The original mutant plant had about 150 commercial leaves as contrasted with a general average of about 25 leaves per plant of the variety from which it originated.

The flowers of this variety averaged 5 petals, 5 calyx lobes, 5 stamens and a two-lobed pistil per flower, while the mutant race had single flowers with a much larger number of floral parts, such

as 20 petals, 20 calyx lobes, 15–22 stamens, and as high as 18 pistil lobes. When both the parent and the mutant races were grown side by side under a variety of similar environments, this great series of character differences persisted, making this case perhaps one of the most striking single mutations known (Fig. 673.) In animals, mutations are illustrated by albino robins, sparrows, white elephants and mule-footed hogs, while in human beings, some types of dwarfs (midgets) and albinos are examples which most of us have known.

Types of Mutation.—There is some confusion at present in the literature as to what a mutation is, owing to the increase of knowledge concerning this class of phenomena and a consequent attempt to re-define the term. From a general standpoint, mutations are referred to two types—bud sports (somatic, vegetative, or bud mutations) and seed sports (germinal or seed mutations). A bud mutation appears as a bud or a branch differing in its gene constitution from the rest of the plant. A germinal *mutant* (an organism resulting from mutation) arises from genetic changes first expressed through the development of a seed, producing an entire plant differing genetically from all the other plants of a pure breeding strain. Common illustrations of bud sports are found in azaleas, chrysanthemums, and peaches. In azaleas, pink flowered plants often have a branch with dark red flowers, while in chrysanthemums, white flowered plants have branches with colored flowers or vice versa. Peach trees not infrequently have branches with nectarines, which are essentially peaches devoid of pubescence or with smooth skins. Bud sports may be propagated vegetatively (buds, grafts, slips) and will generally remain as true to type as though they had originated and been isolated through selection by seeds. In fact, many of our commercial varieties of plants have been secured through this type of variation. The California navel orange (Washington navel) is said to have been found as a bud sport on an orange tree in Bahia, Brazil, which for the most part bore oranges with seeds. The Marsh variety of grapefruit, which is ordinarily seedless, is said to have given rise to a variety with fruits full of seeds through a bud sport.

Mutations are more commonly found, however, as seed variations. Many double flowered varieties have arisen in this way.

FIG. 673.—Typical specimen of a fasciated variety of tobacco, which arose as a mutation.

Thousands of different varieties of plants, valuable commercially, have undoubtedly come into being by this process, though, as yet, so little is known concerning the causes of mutation that new types of mutants cannot be artificially produced, although the production of types already known apparently can in some cases be accelerated by the use of chemicals. The experimenter either finds them usually as single plants in large cultures of a variety or they are found accidentally by some interested party,

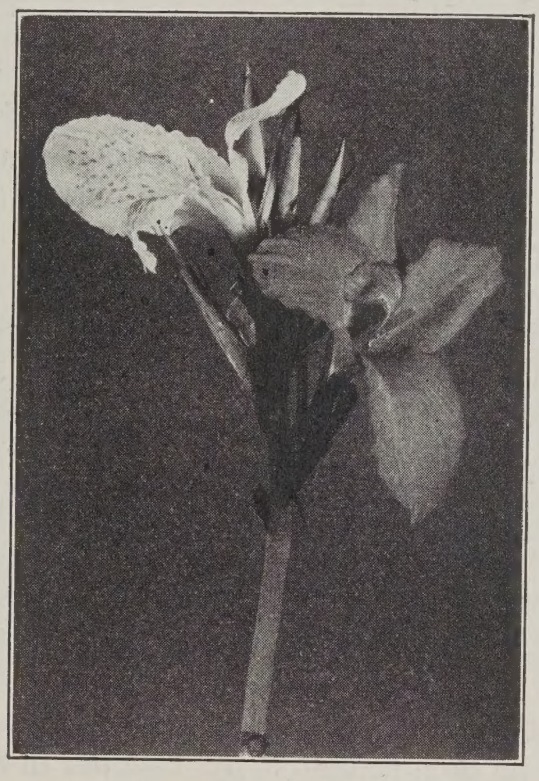


FIG. 674.—Bud sport of Yellow King Humbert Canna. Upper flower yellow and typical of variety, lower flower orange red.

either in the wild or in cultivated plots and propagated for their peculiar or desirable new character. The red sunflower now sold by seedsmen was derived originally from a wild mutant found in Colorado. The wrinkled seed and dwarf habit characters of peas undoubtedly originated from mutations, though when this occurred is unknown. The two flower-color forms (red and cream) of dogwood (*Cornus florida*) probably resulted at some unknown time from mutations from the ordinary white-flowered type.

Mutations, on the assumption that chromosomes are the main bearers of inheritance, may be referred to four or possibly five classes, only the first class of which is definitely known to occur as *either* a bud or a seed mutant. These classes are:

1. Change in a single gene or factor. This is by far the most common type, as demonstrated by the mutants of maize and the vinegar fly, (*Drosophila*). It is the type which largely accounts for the great diversity of organic life, both wild and tame.

2. Duplication of the normal chromosome number as a permanent inherited characteristic, as in the case of *Oenothera gigas* discovered by de Vries. Other examples occur in Primula, the jimson-weed (*Datura*) and in a giant form of Narcissus. This type of mutation, though much less common than the preceding, may have been of great importance in the evolutionary development of such genera as *Rosa*, *Triticum* (wheat, emmer, spelts), *Crepis* and others. This increase in the number of chromosomes generally causes an increase in cell size, resulting in a proportionate increase in the size of the various plant characters, such as flower size, height, and stem thickness. Usually no "new characters" appear.

3. Addition by duplication of a single chromosome, thus adding an extra chromosome to the regular number. In *Datura* as described by Blakeslee and Belling, this has taken place for each of the 12 gamete chromosomes, producing in each case a different type.

4. Marked increase in size of chromosomes as compared with the usual type as demonstrated by Tischler in a giant form of a species of grass of the genus *Phragmites*.

5. "Deficiency" or the loss of a particular portion of a chromosome as found by Bridges in the vinegar fly, *Drosophila*. In general, mutants are more easily distinguished from variations due to crossing when the experimental cultures under observation belong to species with flowers that are ordinarily self-pollinated (pollinated with their own pollen before the flowers open), such as garden peas, sweet peas, wheat, and commercial tobacco. Plants that are commonly cross-pollinated such as maize, apples, and plums are usually very heterozygous unless inbred for a number of generations. Illustrations of mutation in peas are plants with yellow pods, plants with leaves devoid of "bloom,"

and seeds that adhere when mature (chenille), and plants with acacia leaves, *i.e.*, leaves without tendrils.

Generalizations Concerning Mutations.[1]—1. Very little, if anything, is known of the mechanics of mutations, that is, of what causes them, or of the nature of the hereditary materials (genes) which are responsible for them. The genes appear to most students of biology to act as though they were particles or parts of a chromosome.

FIG. 675.—Chenille peas. (After Philippe de Vilmorin.)

2. Most mutants are exceedingly stable, *i.e.*, they retain their new mutant character through many generations.

3. Studies by Altenberg and H. J. Muller on the genes of the vinegar fly, *Drosophila*, indicate a minimum stability on the average for each gene comparable to that of radium atoms, which have a so-called "mean life" of about 2000 years.

4. Certain types of genes apparently are much more changeable than others, so much so that mutants arising from such types appear unfixable. Illustrations of these are frond mutations in

[1] A paper by H. J. Muller (Eugenics, Genetics, and the Family **1**: 106-112, 1923) has been freely used in writing this survey.

the Boston fern, calico variegation of pericarp in maize, color variegation in four-o'clock flowers, bar eye in *Drosophila* and purple-pod color in garden peas. These have a mean life of only a few years. The results of Zeleny for bar eye in *Drosophila* indicate a mean life of 65 years.

5. Slight progress, if any, has been made toward the production of new mutations through the use of external agents (radium rays, X-rays, ether, various chemicals, changes in temperature, etc.). Experiments by Mavor and others do indicate, however, that the rate of production of mutant types already known in a species may be perceptibly increased.

6. Mutative changes are often referred to as losses, though whether this means simply a change of a dominant to a recessive condition, an inhibition or suppression of any gene activity, or an actual loss in terms of inheritance-bearing material (chromatin) has never been made very clear. As pointed out by Morgan, Muller and others, these changes are not all of a loss character, as shown by the occurrence of reverse mutations.

7. As a general proposition, mutations within a given species are liable to occur in any direction and effect any part of the plant's structure. The plant and animal species most thoroughly studied from this standpoint over a comparatively long period of years, show changes in all directions, though changes of a similar character may recur more often as regards certain characters than others. In other words, the rate of mutability varies as regards single genes. Many of these gene mutations may occur and remain unexpressed until a favorable environment is encountered, as would be exemplified in the *Primula* case previously cited, providing the species always grew naturally in a temperature of 30–35° C., for there are other *Primula* forms which, grown at either of these temperatures, remain white-flowered. Gene-mutations then, are to be regarded as largely "fortuitous" (due to chance), as scientists use this word, rather than "directed" toward a definite goal (*orthogenetic*).

8. A single gene-mutation may effect a small or large visible change as regards a single character, or it may result in a large number of changes in the characters of an organism. Mutations may be either very striking (large), or very insignificant (small). The fasciated tobacco mutant, previously cited, exemplified

from one viewpoint a large change, while such chlorophyll mutations as have appeared in corn, barley, and peas, in which the green foliage color has been replaced by various kinds of yellow and yellowish green foliage, are illustrations, from the same angle, of comparatively small changes. What constitutes "large" and "small" changes, however, very much depends on viewpoint. In inheritance studies in garden peas, the hereditary substance that brings about salmon-pink flower color also changes purple pods to bright red pods, brown-gray seed coats to reddish gray seed coats, purple stipple-dot pattern on the seed coat to red stipple-dot, and purple leaf axils to bright red leaf axils. These are always inherited together as a unit so they are regarded as the hereditary expression of one gene, and the evidence indicates they all originated as one mutation. The mutant tobacco type mentioned on page 962 is also an illustration of the numerous changes that have resulted from one gene-mutation. In this case practically all the more general organs were altered—flower parts, number of leaves per plant, shape of stem, and even numerous cell organization irregularities.

9. Mutations usually occur one at a time. In other words, two or more genes in a given plant are not likely to mutate simultaneously; though rare cases of this kind have been noted in the vinegar fly and in cereals.

10. Where a pair of the same kind of genes are together in the same cell, as occurs in all plants breeding true for a certain character such as yellow pod color in garden peas, mutations are only known to occur in one member of the pair, not in both. Data on this have been secured from corn, portulaca, and the vinegar fly.

11. All the accumulated data from a quarter of a century of scientific experiment and observation with many kinds of plants and animals indicate that mutative changes are not restricted to any definite period of the organism's life, though there is some evidence showing that mutations are more frequent during each reproductive or fruiting period.

12. Mutative changes are generally recessive. This is markedly the case in the vinegar fly, *Drosophila*. In such plants as the garden pea, corn, and sweet pea, which have been the subject of intensive genetic investigation, this statement is also strikingly the rule. There are a number of cases in plants

which, so far as known, have not been studied genetically, but which, on general considerations, may be assumed to have arisen as dominant mutants. Examples of these are the cream and red flower forms of *Cornus florida*, the pink flowered form of the lily-of-the-valley and the four o'clock, certain colored flowered bud-sports of the chrysanthemum,[1] and the seeded bud-sport of the Marsh seedless grapefruit.

13. Mutations in general take away from rather than add to the ability of the organism in which they occur to survive. This explains why most cultivated varieties of plants could not compete either with their own wild ancestors in their original home, or with wild plants under natural conditions. The wild organism, under natural conditions, has attained its adaptability through generations of rigid selection and elimination, hence an upset in this balance through even a single mutation is likely to place it upon a very adverse footing as a competitor. Striking examples of such mutants are those which effect the chlorophyll-starch producing mechanism in corn, peas, barley, tobacco, resulting in yellow or albino foliaged types, some types of which never live long enough to flower and fruit.

14. Bud-sports are believed to be very rare in such plants as the strawberry, apple, and potato, while they are comparatively common in many ferns, in dahlias, in chrysanthemums, and in citrus fruits. Bud-mutants, however, are very rare, as compared with mutations arising through seeds.

[1] Yellow and red-flowered chrysanthemum bud-sports from white-flowered varieties may have arisen not as gene mutations, but as variations from hybrid plants heterozygous for these colors, in which white color was dominant.

CHAPTER XLI

THE PHYSICAL BASIS OF HEREDITY

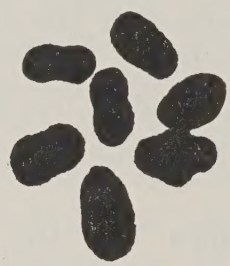
The Physical Basis of Heredity.—The natural consequence of the rediscovery of Mendel's laws and the study of mutations was a search for a cell-mechanism that could bring about these phenomena. Students of the cell had long been accumulating a mass of facts and hypotheses which, at this juncture, were highly suggestive to geneticists, but the particular cell-organs or bodies that appeared to meet the needs were the chromosomes, referred to in Chapter II. The zoologist, Sutton, and the botanist, Cannon, were among the first to point out definitely the relation of chromosomes and the reduction divisions to Mendelian segregation.

Chromosomes.—Chromosomes are the most striking and permanent features of nuclear organization. Figuratively, if not literally, these self-perpetuating nuclear bodies represent most of that which is truly immortal in the individual organism's physical make-up, whether human being, plant, or ordinary animal. Like fleets of little canoes, they have carried their precious freight of genes down the stream of descent through generation upon generation from the beginning of life. In that long voyage many cargoes have been lost in part, or become modified, or have even been transhipped, but there is every reason to believe that many of the genes of these cellular fleets were hoary with age when man first emerged as a species. As observed in dividing nuclei, chromosomes are various in form, but are usually somewhat rod-like. They are constant in number for every body-cell of a given variety or race, and half of them were derived from the male parent and half from the female parent. No matter how different the great mass of cells making up the individual plant or animal body (excepting the gametophytic generation in plants and the eggs and sperms in animals), they always have the same chromosome number.

Chromosome Numbers.—In the onion, the body cell (often referred to as the somatic, 2 x, or 2 n cell) chromosome number is 16, in garden peas and sweet peas, 14, in some types of wheat 28, in commercial tobacco 48, in nightshade (*Solanum nigrum*) 72, in some ferns 128, in the vinegar fly (*Drosophila*) 8, and in man probably 48. In a few species of animals, the male and female differ by one chromosome, and in many bees and ants the males have only one half the female number because they develop from unfertilized eggs—they have no paternal contribution.

The Reduction Divisions.—Excepting the sperms and eggs of animals and the whole gametophyte generation (pollen grains and embryo-sacs in the higher plants) in plants, the cells of an

FIG. 676.—The reduced number (7) of chromosomes of the garden pea. (After W. A. Cannon.)



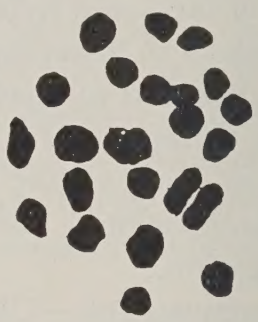


FIG. 677.—The reduced number (24) of chromosomes in commercial tobacco, *Nicotiana tabacum*. (Two in the center are partly superimposed.)

organism always have the same number and each dividing cell halves each chromosome for its two daughter-cells so that each body-cell is assumed to have the same chromatin constitution. Previous to the formation of the germ-cells in animals and to the gamete-producing pollen grains and embryo-sacs in the higher plants, a peculiar and very important phenomenon, known as *reduction*, occurs during which the chromosome number is reduced by half as the result of two successive cell divisions, the first of which brings about the separation of whole chromosomes, so that in such a plant as the garden pea, the cells resulting from this first reduction division each contain only 7 of the 14 chromosomes of the body cells. This first division (Fig. 678) is technically called the heterotypic or differential division because the two daughter-cells originating through it are assumed to be

qualitatively different in their chromatin constitution. For the chromosomes of the ordinary body-cells are believed to occur in pairs, and the two members of the pair are homologous in fundamental make up, *i.e.*, as to their genes. There are many reasons for believing this, both from data accumulated through genetic experiment and from cytological observation, one of which is their similarity in shape and size. In *Drosophila* there is one large pair, two medium sized ones, and one in which the chromo-

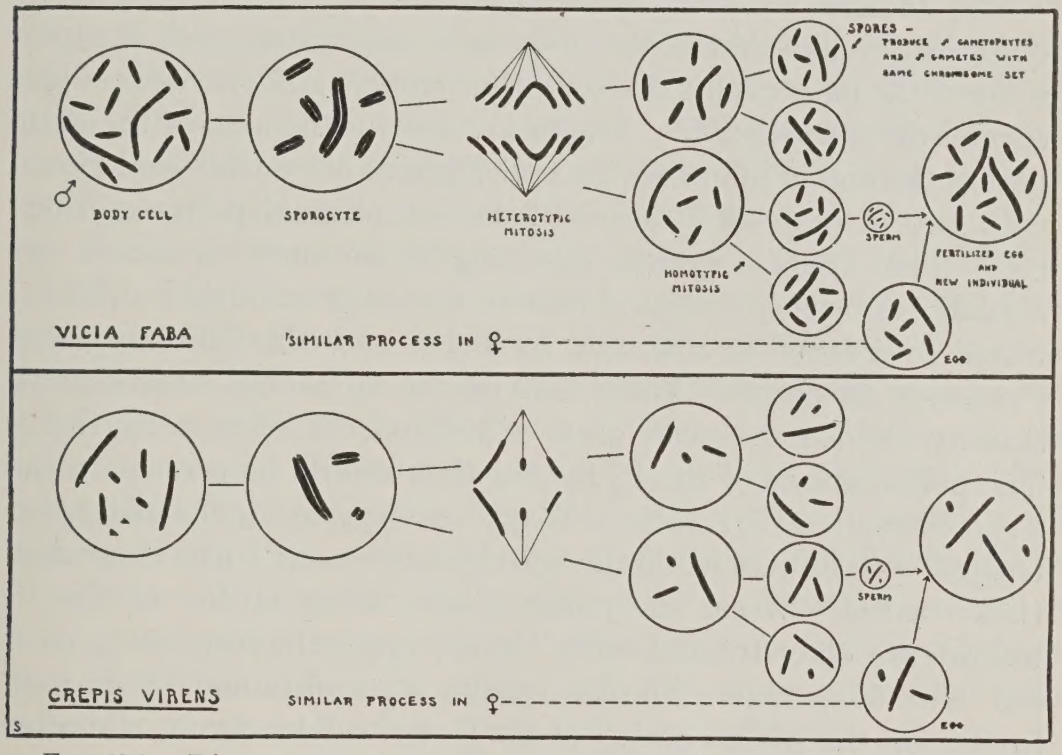


FIG. 678.—Diagram of chromosome cycles in *Vicia faba*, the broad bean, and *Crepis virens*, a relative of the dandelion, showing pairing of those chromosomes alike in size and composition, as well as the reduction divisions and fertilization. (From L. W. Sharp, Cytology. Copyright, McGraw-Hill Book Co. By permission.)

somes appear as small spheres. In certain hybrids between different species of fish in which the chromosomes of each species differ strikingly in size, the cells of the hybrids show both types. A similar case has been described for a species-hybrid of the sundew (*Drosera*), where not only is there a chromosome size difference, but also a distinction in numbers, one parent having 40 short ones, the other 20 long ones. In the formation of the hybrid, one parent contributed sperm-cells with 10 long chromosomes, the other eggs with 20 short ones. In the hybrid cells are

30 chromosomes, 10 pairs of one long and one short, and 10 unpaired shorts. Detailed evidence of this kind has been accumulated from a large number of sources. Suffice it to say there is no evidence extant against the hypothesis that the body-cell chromosomes of a plant or animal occur in homologous pairs. That these pairs are separated and go at random to either pole during the heterotypic division is also supported by a large and constantly increasing body of facts.

The second reducing division, known as the *homotypic*, is quantitative like that of the body-cells, and halves each chromosome of the heterotypic division, thus resulting in two cells of like chromatin constitution. The final result in the case of the male part of the higher plants is four pollen grains of two different kinds, with two of each kind derived from the original pollen-mother-cell. That pollen grains resulting from such divisions are actually different, as stated above, has been strikingly substantiated by Parnell in rice, and by Brink and MacGillivray,[1] and Demerec[2] in maize. Waxy endosperm in maize crossed with starchy endosperm races gives a 3 starchy:1 waxy ratio in F_2. The pollen grains of the F_1 hybrid then should be present in the F_1 anthers in a 1:1 ratio. Waxy endosperms turns red when treated with iodine, while the starchy endosperm turns blue when thus treated. When the pollen grains of an anther of the F_1 hybrid are thus treated with iodine, approximately 50% turn red and 50% blue. Similar results were obtained by Parnell in rice on the pollen grains of an F_1 hybrid involving a similar expectation. The state of affairs as regards the megaspore which eventually gives rise to an egg-cell is somewhat more complicated, since only one of the four megaspores of a single megaspore-mother-cell normally develops, the other three being reabsorbed. The single megaspore, however, has an equal chance in most cases of being one or the other of two kinds.

Cytoplasmic Inheritance.—Other than the chromosomes, no cell structures appear to furnish a basis for the transmission of

[1] Brink, R. A., and H. J. MacGillivray. Segregation for the waxy character in maize pollen and the differential development of the maize gametophyte. Amer. Jour. Bot. **11**: 465–469. 1924.

[2] Demerec, M. A case of pollen dimorphism in maize. Amer. Jour. Bot. **11**: 461–464. 1924.

factors, with the possible exception of the plastids in the cytoplasm. A case of this kind described by Baur occurs in *Pelargonium*, involving plants with white branches, green branches, and branches in which the green and white form a mosaic. Each type, when self-pollinated, gives progeny after its own type, while green branch × white branch, or vice versa, always give F_1 plants entirely green foliaged. The tentative explanation advanced assumes that both sperm cells and eggs may transmit plastids. In cells with both types of plastids, unequal distribution of them in dividing cells will, in extreme cases, result in cells pure for each type, this giving rise to branches either entirely with white foliage or with all green foliage. Other cases which at first appeared inherited through the cytoplasm have been satisfactorily explained on the chromosome hypothesis.

Chromosomes and Genes.—In preceding pages two different kinds of facts have been dwelt upon. One set was derived from breeding experiments and deals with the inheritance of factors, while the other set is based on a cytological study of cells and cellular mechanisms, chiefly involving the activities of the chromosomes. These two sets of facts and their attendant hypotheses appear, when correlated, to be different parts of the same story. The members of a factor pair are distributed at random. So are the two members of a homologous pair of chromosomes. Some pairs of factors, such as those for tallness *vs.* dwarf and green *vs.* yellow pod in peas, are inherited independently of each other. Similarly, chromosomes are assorted independently. The natural inference from these facts is that the chromosomes are the bearers of the factors. Other groups of facts tend more and more to support this idea. Particularly is this true of four post-Mendelian generalizations known as linkage, crossing-over, the limitation of the linkage groups, and interference, largely derived from experiments by Morgan and his co-workers with *Drosophila*.

When a variety of garden pea breeding true to round cotyledons (RC) and tendrilled leaves is crossed with a variety breeding true to wrinkled cotyledons (WC) and non-tendrilled leaves, the F_1 plants all have round cotyledons (RC) and tendrilled leaves, these being dominant. In the F_2 generation, however, each pair of characters—round *vs.* wrinkled, tendrilled *vs.* non-tendrilled—

considered separately, give the ordinarily expected simple *monohybrid* (hybrid for one pair of factors) ratio of 3:1. When both pairs are considered together, the expected *dihybrid* (hybrid for two pair of factors) ratio, if the pairs are inherited independently of each other, as is the case with those tested by Mendel, should give an F_2 ratio of 9 RC tendrilled:3 RC non-tendrilled:3 WC tendrilled:1 WC non-tendrilled.

But in this case these results were not obtained. Vilmorin and Bateson who first studied this cross, discovered that most of the

FIG. 679.—Acacia (non-tendrilled) leaved type (left), and tendrilled leaved type (right) in the garden pea. For wrinkled and smooth seeds, see figure 670. Acacia leaves are linked with wrinkled cotyledons, while tendrilled leaves are linked with smooth cotyledons.

F_2 plants were either round cotyledon and tendrilled or wrinkled cotyledon and non-tendrilled, like one or the other of the grandparents, while a very few plants represented the two expected middle new combination classes—round cotyledon and non-tendrilled, wrinkled cotyledon and tendrilled. 2065 such F_2 plants were distributed thus:

Obtained 1466 RC tend:20 RC non-tend:15 WC tend:564 WC non-tend.

Expected 1162 RC tend:387 RC non-tend:387 WC tend:129 WC non-tend.

The F_2 dihybrid ratio actually obtained when reduced to its simplest terms approximated 11.36:0.15:0.11:4.37 as compared with the expected 9:3:3:1.

When constant races of the two new combinations viz. wrinkled cotyledons tendrilled and round cotyledons non-tendrilled are crossed the two middle terms of the above ratio are greatly increased, while the end terms are much depleted, as shown in the actual results obtained by Pellew:

Obtained 502 RC tend:270 RC non-tend:264 WC tend:0 WC non-tend.

Expected 583 RC tend:194 RC non-tend:194 WC tend:65 WC non-tend.

The results obtained in the first cross illustrate *linkage*, or *coupling* as it was named by Bateson and Punnett who first discovered it in sweet peas. It is called linkage because the two pairs of characters—round cotyledons and tendrilled leaves on the one hand, and wrinkled cotyledons and non-tendrilled leaves on the other hand—for the most part remain associated in their inheritance, *i.e.*, they entered the cross together and in F_2 segregated as though they were partially coupled. The results shown by the second cross also illustrate linkage (sometimes called negative linkage), although referred to by Bateson as *repulsion*.

On the chromosome hypothesis, as largely worked out by Morgan and his co-workers, both coupling and repulsion are linkage, linkage itself being brought about because the factors for round cotyledon and tendrilled leaves are parts of the same chromosome, while the factors for wrinkled cotyledons and non-tendrilled leaves are located in the homologous chromosome of this pair. The presence of the middle terms of the ratio in the first type of cross described is due to *crossing-over*, and such individuals are known as *cross-overs*, while the two end terms—RC tendrilled and WC non-tendrilled—are called *non-cross-overs*. The linkage in this illustration, as is commonly the case, is only *partial*, the cross-overs here amounting to about 3%. Crossing-over is assumed to be brought about during certain stages preparatory to the first reduction division in the formation of the germ-cells, when the members of each pair of homologous chromosomes become closely associated and in many cases twist about each

other. When the separation phase comes, instead of untwisting and separating in their previous entirety, portions of the homologous chromosomes are exchanged, and with these exchanged chromosome portions go the factors making up that part of the chromosome. *Crossing-over, then, is the process of exchanging factors of a pair of homologous chromosomes through the exchange of chromosome portions* (see Fig. 680).

Generalizations on Crossing-over.—The per cent of crossing-over, while relatively stable for any specific case, is influenced by changes in temperature, by age, and by the influence of X-rays, but is independent of the way in which the factors enter an individual. Definite genetic factors, having so far as known no other visible expression, also in certain cases cause variation in the percentage of crossing-over. The length of the chromo-

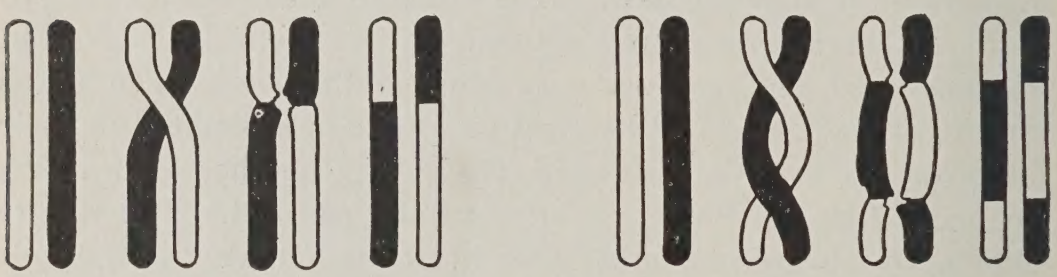


FIG. 680.—Diagram illustrating the theoretical behavior of the paired homologous chromosomes in crossing over (see text). Single crossing over at left; double crossing over at right. (After Babcock and Clausen from L. W. Sharp. Copyright, McGraw-Hill Book Co. By permission.)

somes, as will seem logical from later statements, also increases or decreases the general amount of crossing-over, as the genes are close together in short chromosomes and the chromosomes themselves are less liable to twist and break, as exemplified by the short pair in *Drosophila*. Genes close together show less crossing-over than those far apart. Crossing-over only takes place in the female in *Drosophila*, while, in the silk-worm crossing-over occurs only in the male. In the grouse locust (*Apotettix*) Nabours found it took place more frequently in the female than male. In all investigated cases in plants, both sexes are equally involved. When crossing-over reaches 50% the ratios are indistinguishable from those of independent assortment. Each "break" in a chromosome pair is counted as a cross-over, hence

if two "breaks" occurred in a chromosome pair, the result might be only an exchange of a single chromosome section from the middle, but this would be referred to as two "breaks" or a *double cross-over.* Data from *Drosophila* show that not single genes or factors are exchanged in crossing-over, but that whole blocks of genes or whole sections of chromosomes have been lost—in other cases added, these conditions being first suspected through experimental data from breeding and afterwards confirmed cytologically. The first is called *deficiency,* the second *duplication,* as the factors were found to be duplicated in the latter case.

Linkage in General.—New cases of linkage, in both animals and plants are continually being discovered. There are five linkage groups of 2 pairs each in the garden pea, eight groups of 2 or more pairs each in sweet peas, two of which probably belong together, the linkage being very loose; four in *Drosophila melanogaster;* several groups each in a number of other species of *Drosophila;* seven groups in maize; two of 2 pairs each in the tomato; one group of 3 pairs each in the snapdragon (*Antirrhinum*) and the rat; one group of 8 pairs in the grouse locust (*Apotettix*); one group of 5 pairs in the primrose (*Primula*); one group of 2 pairs in the castor bean, mouse, common bean, silkworm, and pigeon.

There are also numerous cases of sex linkage (*i.e.*, factors occurring in the same chromosome with the factor that conditions sex) in moths, poultry (6 factors), canary, fish, cat, man, red campion (*Lychnis dioica*), and *Bryonia.* In poultry there is one important linkage involving high winter egg production and sex, discovered by Pearl. In man there are a number of sex-linked factors, notably color blindness (the inability to distinguish sharply between red and green) and bleeding or the inability of the blood to clot easily (*Haemophilia*) which apparently are only transmitted through the daughters to the grandsons and never through the sons. These characters are rarely present in females since to have them they must inherit them from both parents.

Limitation of the Linkage Groups.—If the assumption that the chromosomes are the bearers of the factors of heredity is true, precisely this phenomenon of linkage should be expected, and

the number of linked groups should equal that of the chromosome pairs. Peas which have 7 pair of chromosomes should have seven such linked groups, sweet peas 7, tobacco 24, nightshade 36, and the vinegar fly, *Drosophila*, 4. In other words, all the factors of a plant or animal should be linked together in groups, and these groups should equal the number of chromosome pairs. If the groups are found to be greater in number, after all the possibilities have been exhausted, after every possible precaution has been taken—perhaps then other explanations must be looked for or new subsidiary hypotheses be devised. But in the case of *Drosophila*, the number of linked groups do correspond with the number of chromosome pairs. In this organism, the linkage relations of between 300 and 400 factors have been studied and these all have been found to belong to four groups. Three of the groups have a large number of factors, corresponding roughly to the three large pairs of chromosomes, while one group consists of only three linked factors and corresponds to the small spherical pair of chromosomes. Every factor in a group is linked with every other factor in that group by their presence in the same chromosome. Hence, there are over fifty such linked factors in the sex chromosome. All these factors are referred to as *sex-linked*, because of their association in the same chromosome with the differential factors for sex. Recent studies by Punnett have demonstrated eight groups of linked factors in sweet peas, one of which he believes may be loosely linked to one of the other seven, so that in sweet peas, as in *Drosophila*, the number of linked groups probably corresponds to the number of chromosome pairs.

The Arrangement of the Genes.—Assuming that the chromosomes are the bearers of the factors or genes, which most students of genetics now admit is most probable, the question arises as to the arrangement of the genes in their respective chromosomes. From data largely amassed from experiments on *Drosophila*, the genes appear to be arranged serially in constant, unvariable, linear order in each chromosome, each gene having its particular place (*locus*) which it or its homologous substitute always occupies, much as different types of beads might be strung on a string in a definite order of sequence. The *loci* of a pair of homologous chromosomes are then also paired homologously, occupying loci

opposite each other. Of some significance in this connection is the fact that in some cases, chromosomes have been observed to be made up of small particles called *chromomeres* and that these too are linearly arranged. Determining the spatial relations of the loci of factors or genes to each other is called *mapping the chromosomes.* The unit of measurement is based on 1% of crossing-over, but 1% of crossing-over may represent different morphological distances in different chromosomes or in different portions of the same chromosome. Expressed in units equal to 1% of crossing-over, Morgan and his co-workers have graphically pictured in comparative fashion, the lengths of the four pairs of *Drosophila* chromosomes, thus: chromosome I, which contains the sex-linked factors, is 68.0 units long; chromosomes II and III, so far as determined, are 105.0 and 101.0 units; while in chromosome IV, the small spherical one, no crossing-over so far is known.

Interference.—Crossing-over in one region interferes with another crossing-over taking place nearby, and this is technically referred to as *interference.* Morgan illustrates this phenomenon by showing what takes place as regards the cross-over relations of the three *Drosophila* factors, sable (a body color), bar (a factor affecting the shape of the eye), and vermilion (a factor conditioning vermilion eye color). Vermilion, sable, and bar form a linear sequence in the order named, the distance from vermilion to sable being 10 units, and from sable to bar 14 units. Crossing-over between vermilion and sable results in a decrease in crossing-over between sable and bar of 10% the usual percentage of crossing-over between these two factors when considered alone being 14%. Hence crossing-over in one region protects the nearby region, until the distance becomes great enough so that its protection value vanishes, which in chromosome I of *Drosophila* is about 46 units, according to Weinstein. He finds, however, that as the distance becomes still greater, the protection value reappears. This phenomenon is one of the strongest supports of the linear arrangement hypothesis. Interference is explained by the twisting of the pairs of chromosomes around each other during certain stages of the first reduction division. At the points where they cross, breaks occur, and thus crossing-over is accomplished. But the breaks occurring at these points

naturally tend to *interfere* with breaks at nearby points that might have occurred, since there is a limit to the number of twists within a given distance.

Multiple Allelomorphs.—Heretofore all our illustrations have dealt with factors related allelomorphically to each other in their inheritance in pairs. But there are cases known in Drosophila, peas, grouse-locust (*Apotettix*), maize, columbine (*Aquilegia*), rabbits, mice, and the red campion (*Lychnis*), common beans, silk-worm, and others that involve an allelomorphic relationship of more than two factors. In the bean, as found by Emerson, there are three such factors. These give rise to green foliage with green pods, green foliage with yellow pods, and yellow foliage with yellow pods. In peas there are three in the same series, one green foliage and two different types of yellow foliage. In the grouse-locust series, worked out by Nabours, there are fourteen, each concerned with an all-over body pattern. The peculiar fact concerning these various cases is that any pair in the series when crossed gives a simple monohybrid ratio in F_2. In the case of the beans, green foliage with green pods $\times$ green foliage with yellow pods in F_2 gives 3:1, while any other combination of the three will also give the same result. The explanation of this phenomenon lies in the assumption that each member of the allelomorphic series has resulted from a mutation at the same chromosome locus. Locus A, then, would give rise to A^1, A^2, etc. These several distinct mutations at the same locus occur independently, in no sequence (as regards their dominance relations) and at different times and places. Only two of them can be combined in one hybrid organism at a time.

CHAPTER XLII

GENERALIZATIONS AND SPECIAL CASES

Heterosis or Heterozygosis.—For a half century or more, plant and animal breeders have noticed that inbreeding often results in a variety or breed deteriorating and conversely that crossing relatively unrelated races very often produced exceptionally vigorous offspring. These facts formed the basis for that well-known generalization by Darwin: "Nature abhors self-fertilization." But modern genetic studies have demonstrated that inbreeding in itself causes no marked deterioration if the race had a vigorous genetic constitution to start with, and again conversely, that crossing will not produce more vigorous offspring, unless the races are of different genetic constitution. But geneticists have repeatedly found in pedigree culture breeding that F_1 generation hybrids between two races breeding true for a number of differential factors, were often larger in size or weight, more vigorous, more floriferous, more productive, or attained maturity more rapidly, and this effect is known as *heterosis* and is believed to be due to the heterozygotic condition of the factor pairs of the individuals showing this condition. Striking examples of this fact are to be found in crosses of varieties of maize, tomato, cucumber, and castor bean, species of walnut, Prunus (Compass cherry), tobacco, hybrids of the ass and horse (mule), and crosses of different breeds of poultry. No doubt many varieties of herbaceous and woody plants propagated asexually, for ornament and fruit, owe part of their value to heterosis, for it is well known that many of such varieties are in a highly hybrid state as evidenced by the great variation in, and the relatively poor, worthless quality of most of their offspring. Increase in yield in corn by the use of first generation hybrids secured by planting two varieties in alternate rows and detasseling one was first demonstrated by Beal (1876–1882).[1] Interest was again awak-

[1] Beal, W. J. Reports, Michigan Board of Agriculture, 1876, 1877, 1880.

ened in this subject by the publications of East (1908), Shull (1908, 1909), Collins (1909, 1910), and others (Figs. 681, 682), resulting in various practical applications, especially through the

FIG. 681.—Shows inbred strains of corn and increased vigor and production of stalk from crossing them. Two inbred strains (left). First generation hybrid offspring from crossing them (right). (After East and Hayes.)

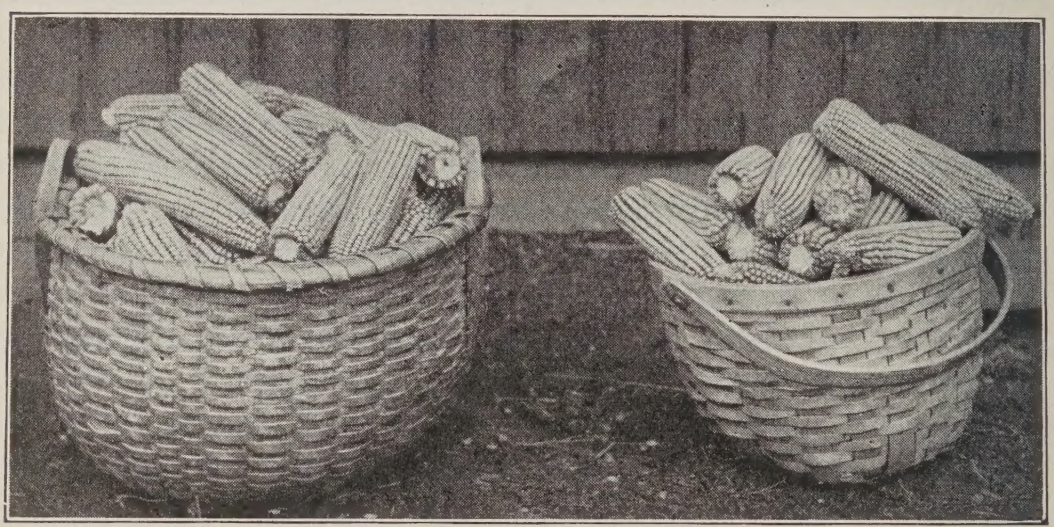


FIG. 682.—Results in ear yield of crossing two inbred varieties of corn. Average of parents after 3 generations of inbreeding, 61 bushels per acre (right). Crop of first generation cross of inbred varieties, 101 bushels per acre (left). (After East and Hayes.)

modified methods for growing seed of crossed corn, devised by D. F. Jones. Growing tomatoes and cucumbers from hybrid F_1 seed has also been found commercially profitable, because of the

greatly increased yields secured. F_1 poultry, derived from crossing certain breeds, has resulted in securing the same weight in a shorter time, while the case of Burbank's walnut hybrids and the rapidity with which the F_1 trees grow, is notorious, as is also the well-known "toughness of the mule." Flowering plants often are much more floriferous—"they bloom themselves to death," as the growers say, from this cause. But there are limits in genetic difference beyond which the results may be the converse of what is stated above, due to another set of phenomena. While some F_1 species hybrids show marked heterosis, others show marked debility. Their growth is slow, they are constitutionally sickly. They never reach the heights their parents have. Subsequent generations grown from the F_1 plants continuously decrease in heterosis and heterotic effects or characteristics such as yield, rapidity of growth, etc. In F_1 hybrids between peas, yields as well as height are often strikingly increased.

Generalizations on Factors.—In the foregoing account, the fundamental units of heredity, the factors (genes) and their activities, have been described from many different angles. Our first concepts of them arose largely through the discovery of Mendel's laws. In his classic paper on "Experiments in plant hybridization," they began to emerge as the germ-cell representatives of pairs of contrasted characters, although in reality present but not detectable, in organisms homozygous for each character. The factors are associated in the body-cells in homologous pairs and, during the formation of the gametes preparatory to fertilization, segregation of maternal and paternal factors takes place at random, each as uncontaminated and unchanged as when they first became associated. They are distributed through certain packages or in groups, each group being assorted independently, being distributed at random to either of the two daughter-cells resulting from the first reduction division. All the factors of a given group are always linked; some loosely, others more closely, depending on their proximity and spatial relations to each other. Different pairs of factors in the linked groups have different cross-over values, which are relatively stable and predictable. The number of these linked groups is limited and corresponds in one case, perhaps in two cases, to the number of chromosome pairs. When investigations have progressed sufficiently in other organ-

isms, the belief is widespread that more of such correspondences will be found. The arrangement of the factors is orderly, unvariable, constant, and linear, as demonstrated by the data from crossing-over and interference. After the linkage breaks, during the early stages possibly of the first reduction division, the rearrangement of the factors is still orderly, stable, and linear. In other words, as a general proposition, factors appear always to maintain the same architectural relations to each other. Each has a definite place on the bead string, and though it may change strings, it is nearly always number 2, or 3, etc. on any string.

Many cases of factors are known which not only exist as members of contrasted pairs, but in series, each member of which bears the same alternative, contrasted relation to every other one of the series (multiple allelomorphs). Factors not only have one visible expression, after which they are often named, but in many cases, these are numerous, occurring in any part or in widely separated parts of the organism, and showing only at special or at periodic periods in its life history. Factor expressions are changed, modified, and completely or partially inhibited by the action of other factors (often referred to as the "internal environment"), either singly or in groups, as well as by various changes in external environment. Until the action of various environments on a factor is known, comparative studies should always be made as nearly as is practicable under the same environmental conditions, and the more precisely controlled these conditions are, the better. Factors, as far as their expression in the make-up of characters in the organism is concerned, may be compared to the threads in the pattern of a rug. In one part of the pattern they show; then they apparently are absent, only to reappear again in another place in the design. Many threads take part visibly only once; others many times. For example, in peas, one factor primarily conditions the presence of reddish gray seed coat, reddish streak lines on the stem, red color in the axils, salmon pink flower color. In the presence of two additional factors, the seed coats are stippled with reddish dots and the immature pods are bright red. But though this one factor apparently has so many expressions, it is visible in the architecture of the plant, as is the particular thread in the pattern of the rug, only in certain places.

Many factors act as *lethals*, killing the gametes in which they occur, as in the case of the balanced lethals of *Oenothera*, and the factor for yellow hair pigment in mice. This last case was the first lethal discovered, and it not only expressed itself in its death-dealing character, but as a determining agent for yellow pigment. All mice homozygous for yellow die and the race is carried on through the heterozygous individuals.

Factors are not believed by geneticists to be determiners of the various character expressions with which they are associated in name and otherwise in any simple fashion. Environments and other factors, most of them perhaps unisolated, are always concerned with the end results. No character is simple. Genetic factors of necessity, are differential agents. For example, the green-pod pea variety through mutation gives rise to a yellow pod race. The yellow pod race is differentiated from the green pod race, then, by one factor—the factor for yellow pod. No one knows how many factors are concerned in producing either the green pod or the yellow pod characters, but the difference between them acts as a unit in inheritance.

Factors that bring about the same end result—the same character expression,—may be very different, from the standpoint of origin, their group connections, and perhaps as regards other activities. Examples of this kind are the various lethals. Another illustration is the red bran pigment ("seed coat color") of certain wheats, the inheritance of which was first studied by Nilsson-Ehle. In crosses with certain white "seed" varieties, F_2 ratios of 15 red:1 white and 63 red:1 white were obtained with subsequent F_3 results that demonstrated that 2 pairs or 3 pairs respectively, of independently assorted factors were involved, one member of each pair in each case expressing itself as a dominant red. The Howards in India, and Gaines in Washington obtained similar results. The "reds" generally were indistinguishable whether they were all present, homozygously or heterozygously, or whether just one was present. Two such factors involving black lemma color of oats, have also been found by Nilsson-Ehle. Numerous other cases might be cited, showing the phenomena to be general. The point to keep in mind is that similar character expressions do not necessarily owe their origin to identical factors. This is important from the standpoint of

plant classification, since characters morphologically alike may be geneologically unrelated, just as many chemical combinations produce very similar physical characteristics but these do not demonstrate the presence of the same elements.

Many factors (*complementary* factors) have been discovered that, so far as our very imperfect knowledge carries us, have no expression except when acting together. This fact explains many strange genetic results, such as the production of colored F_1 progeny from crossing two varieties breeding true to non-colored characters. White × white gives colored flowers in certain sweet pea crosses; white × white aleurone gives colored F_1 progeny in certain maize crosses; certain crosses involving a light yellow and a white bean parent give all black F_1 progeny.

Phenotypic ratios involving two pairs of factors are often modified by peculiarities in expression from the ordinary 9:3:3:1 to other proportions, among which are 9:7, 9:3:4 (flower color from pink × white in garden peas), 13:3 (dominant yellow cotyledon × recessive yellow cotyledon in peas giving a ratio of 13 yellow: 3 green), 1:2:1:2:4:2:1:2:1 where each genotypic F_2 class is distinguishable, as in a cross between a fasciated race of tobacco with uncolored sepals (non-calciflory) and a normal race with colored sepals (calciflory).

The factor hypothesis has been found applicable to all types of characters and organisms, whether varieties or species, and whether these are wild or domesticated types. In maize and garden peas, over fifty factors have been investigated, but none of the genetic work has approached the magnitude of that with the vinegar fly.

Chimeras and Graft-hybrids.—Chimeras, as found in plants, are individuals composed of two genetically distinct kinds of tissue. These may have resulted from bud mutations and the subsequent growth of the new type of tissue thus produced along with and interwoven with the older tissue derived from the non-mutated cells. Such chimeras are referred to as *natural*, in contrast with those artificially or experimentally produced. Examples of these are varieties of geranium (*Pelargonium*) having green leaves with white edges; variegated-leaved forms of *Euonymous japonicus*, the four o'clock, snapdragon and others. Varigation in plants, whether in leaves, flowers, or fruits, is not all

chimeric in origin. Some variegation has been shown by Baur to be due to "infectious chlorosis," a diseased condition involving deficiency in chlorophyll, but this disease is not transmitted through the seeds.

The experimentally produced chimeras have resulted in most, if not in all cases, from grafting or budding, and are made up of tissue from two different varieties or species. The best known of these is *Cytisus Adami,* which originated from a graft using purple broom (*Cytisus purpureus*) as cion on a *C. Laburnum* stock. The chimera form has an outer layer of *C. purpureus* cells, while all the inner tissue is *C. Laburnum.* Other similar

FIG. 683.—Chimera in apples. Golden Russet and Boston Stripe combined in the same fruit as a result of grafting these two varieties as cion and stock. These "freaks" are explained by the failure of the original buds of the cion to grow, after grafting, and the appearance of an adventitious bud at exactly the juncture of stock and cion, including in itself tissue from both stock and cion. These tissues grow side by side, remaining quite distinct, each tissue of cells reproducing its own peculiar characteristics, the differences becoming striking only in the fruit. (After Castle, from The Journal of Heredity.)

cases are chimeras of pear and quince and peach and almond. Not infrequently grafted apple trees occur, the cion portion of which appears to be in part a chimera. The apples on such trees are usually of three kinds, two of which are the pure fruits of one or the other parent (cion and stock). Some branches, however, produce apples which are part of one variety and part of the other—for example, the calyx-end half will be red and sour, the stem-end half, yellow and sweet. (Fig. 683). Such chimeras are *sectorial,* while the other type is called *periclinal.* Chimeras of this sectorial type are probably the result of "stock" tissue growth, as in the case of periclinal types, until the fruiting period

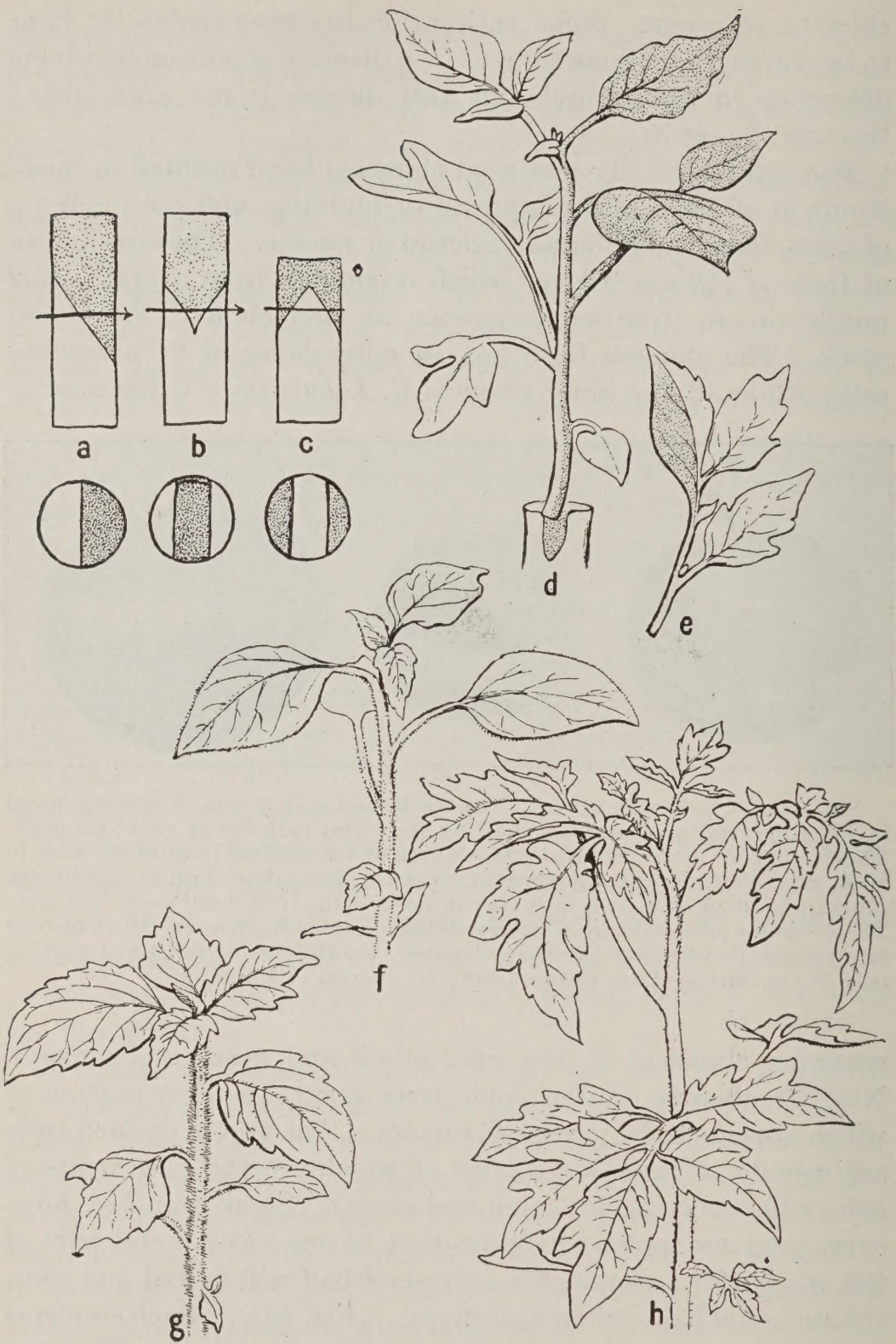


FIG. 684.—*a*, *b*, *c*, Diagrams showing different forms of grafting used in producing Winkler's tomato-nightshade chimeras (graft-hybrids); shaded portions representing cion tissue, unshaded, stock tissue. *a*, Splice grafting. *b*, Cleft or wedge grafting. *c*, Saddle grafting. *d*, Sectorial chimera (shaded portion, nightshade; unshaded portion, tomato tissue). *e*, Chimera leaf, part nightshade and part tomato. *f*, Nightshade. *g*, Chimera (*Solanum Tubingense*). *h*, Tomato. (Adapted from Winkler.)

is reached, when in some cases the two tissues are associated together sectorially. The two tissues, since they are so very similar, possibly grow alongside each other in portions of the tree as sectorial chimeric tissue, unnoticed until the fruiting stage.

Winkler's so-called graft-hybrids are periclinal chimeras and not hybrids at all, according to Baur, who has done much toward the elucidation of chimera phenomena. Winkler produced these chimeras by grafting the tomato and common nightshade (*Solanum nigrum*) together. Along the graft union of the two species (Fig. 684) buds very occasionally arose and grew, which were composed of both tomato and nightshade tissue in various degrees. One type of chimera, very similar in general character to the nightshade, is all nightshade tissue except for a single outside layer of tomato epidermal cells. Another type, resembling the tomato closely (*S. proteus*) is all nightshade except for two outside layers of tomato cells. In two other forms, these tissues are just reversed—tomato inside with a single layer of nightshade outside, and tomato inside, with two layers of nightshade outside. The nightshade cells have 72 chromosomes while tomato cells have 24. In still another type of chimera, Winkler believes there has been a cell fusion between the two species resulting in a true graft-hybrid with 12 + 36 (the reduced germ cell numbers) or 48 chromosomes, but Baur doubts the completeness of the proof, and explains the result otherwise. These chimeras are propagated by slips.

The Limits of Crossing.—The limits within which different species of plants and animals can be crossed and produce living offspring are very ill-defined. If taxonomic relationship (the relationships as given in the floras of different countries and sections of countries) is used as a criterion, the exceptions are comparatively numerous and confusing, except as between the larger groups, such as families. Crosses between species of different genera are very common in some families, especially among the orchids, pinks, amaryllids, and grasses. In other families, generic crosses are very uncommon, and even species crosses are rare. The pea family with its wide cosmopolitan distribution and large number of species is a striking example. In the large genus to which the sweet pea (*Lathyrus*) belongs, there are many other species, but although some of these appear

to be closely related, there seems to be no authentic case of crosses between them and the sweet pea. Other families in which even the known species crosses are rare, comparatively speaking, are those to which the carrot (*Umbelliferae*) and the morning glory (*Convolvulaceae*) belong.

Crosses between members of different families are unknown, except in one very doubtful case. Species hybrids are common, although, as previously mentioned, more common in certain genera than in others. The forms of some genera, such as *Ricinus* (the castor oil bean) and *Zea* (corn or maize), so hopelessly cross that those who classify plants consign all of them to one species, though there are enough striking differences between them to make innumerable species. Striking species-crosses among plants are illustrated by the cultivated roses, many varieties of which have involved in their ancestry at least two species and in most cases, many more. Gladiolus is another well known plant, the cultivated varieties of which contain the "blood" of numerous wild species. Our cultivated plums are often hybrids with the "blood" of three or more species in their make-up.

Species that may be budded or grafted together and flourish as stock and cion often cannot be crossed, *e.g.* lilac on ash, apple on mountain ash, tomato on tobacco, tobacco on potato. Even varieties of the same species in some cases will not cross as is shown by the recent studies on pollination in the sweet cherry (*Prunus avium*).[1] Gardner found that all the varieties with which he experimented set no fruit when the flowers of each variety were pollinated with pollen from the same variety. Further, in some cases when pollen from one variety was used on flowers of another variety, no fruit set.

The student who is interested in this subject of the limits of crossing should consult "Die Pflanzen Mischlinge" by Focke.[2] In this work species-hybrids in great number are listed and described under families.

Why crosses cannot take place, except within comparatively narrow limits, is a fertile field for investigation. In some cases

[1] Gardner, V. R. A preliminary report on the pollination of the sweet cherry. Bull. No. 116, Oregon Agric. Exp. Sta. 1913.

[2] Focke, W. O. Die Pflanzen Mischlinge. Berlin. 1881.

it is the inability of the pollen of one kind to germinate on the stigma of the other kind; in other cases the pollen tube is unable to grow long enough to reach the ovules as in the case of *Mirabilis* species, where the cross is successful when pollen from the long pollen tube parent is used on the short-styled parent, but unsuccessful when the cross is reversed. *Nicotiana glutinosa* will cross with some varieties of *N. tabacum* and not with others. In the pea, one subspecies will cross with certain varieties, and has never been successful with others, and even with the varieties where the crossing has been successful, the percentage of successful trials is very low. This subject is also discussed on page 395.

Perhaps the ability or inability of one form to cross with another may be crudely pictured as the "fitability" or "unfitability" of the parts, as one would find in trying to make a successful machine out of a pile of automobile parts in which all the parts were represented, but 50% of them were one make and 50% of another make. Even if the percentage of one kind were increased to 95, and the 5% remainder represented parts essential for mobility, the machine would be unsuccessful. Even one part, if it were vital to mobility, would make a complete machine impossible.

Sterility.—*Sterility* refers to the inability of an organism to produce offspring after pollination (not necessarily fertilization) has taken place. This term covers a basket full of different phenomena, which so far have been but slightly sorted. All degrees of sterility are found in the F_1 progeny of crosses between different organisms. Constant back-crossing from generation to generation to either of the original parents may result in a *full* or partial return to fertility, but accompanying this return it has been noticed that more and more of the dual characters of the ancestral species have been eliminated. More and more the subsequent progeny tend to resemble only one of the original ancestors, and that ancestor is the one used in the back-crossing. In a cross involving a peculiar variety of pea with shiny purple seed-coats and one of the usual types of garden pea, the F_1 progeny were not more than one fourth fertile (*i.e.*, as determined by the number of peas per pod). Among the F_2 plants were some almost sterile, and others with a high degree of fertility,

although by no means representing complete fertility. The high fertile classes resembled one or the other grandparent, in some cases being almost indistinguishable.

The genus *Nicotiana* has about 45 species. Crosses between them represent all degrees of sterility, from those in which the crossed seed develop only imperfect F_1 embryos that will not germinate, to crosses that give F_1 progeny that are as robust as, or perhaps more so, than the parents, and that are apparently perfectly fertile. Between these extremes are species crosses that give crossed seeds which germinate almost 100%, but live as F_1 plants only a few months and never develop mature, true leaves; species crosses that give F_1 progeny[1] more robust than either parent but almost sterile; that are weak, barely flower and are absolutely sterile; that are similar in robustness to the parents, but only partially fertile. Certain types of sterility may be associated with definite factors, as in the case of the *Drosophila melanogaster* male discovered by Bridges. This male type lacks the chromosome known as the Y chromosome and is completely sterile. But this type of sterility possibly may be of a different category than that involved in species crosses, though this is doubtful. Sterility in species hybrids may not be as simple, but there is little doubt that it too is governed by the interactions of genetic factors. Curiously striking is the great preponderance of sterility in the male in species hybrids in both plants and animals. Detlefsen found the F_1 male sterile and the female fertile in guinea pig crosses. Other cases cited by Babcock and Clausen are *Bibos* sp. × domestic cattle, Bison × cattle, bantung × zebu, wheat × rye (slightly fertile), *Nicotiana tabacum* × *N. sylvestris* (slightly fertile). Many other examples might be cited. One of the rare reverse cases is that of a cross made by Baur of *Antirrhinum majus* × *A. siculum*, in which all the ovules were sterile but a small percent of pollen was fertile.

Selection and the Nineteen Beans of Johannsen.—The selection concept, in the long course of its evolution, has conveyed many meanings. At first the primitive tribesman selected the best wild individual plant of the type he or she was interested in, and planted it near the hut, just as primitive tribes do today.

[1] East, E. M., and H. K. Hayes. Heterozygosis in evolution and in plant breeding. U. S. Dept. Agr., Bur. Plant Ind. Bull. 243. 1912.

In their careless mode of life seeds of this perhaps strewed the dooryard, grew, fruited occasionally, and all but the best were cleared away in the occasional clean up of hut surroundings. For countless ages selection of this type went on, and still goes on. Half a century or so ago Darwin and others crystallized this idea into the theory of evolution, making Nature herself take the place of the tribesman. Thus evolved the hypothesis of Natural Selection. Natural selection was conceived by Darwin and Wallace to have built up all the multitudinous forms of the organic world from very simple beginnings through this general process. And if its effectiveness was so great in nature, naturally man could, given enough time, accomplish similar "miraculous" changes. A species or variety could be continuously improved in a desired direction by constant selection of minute differences each a step along the road toward the perfectly adapted type. The information from practical breeders of all types seemed to support this idea, as many crops and breeds of animals had been or were constantly being evolved and made more perfect. Through this principle of selection, the sugar beet had been increased in sugar content from 6.2% (Marggraf, 1745)[1] to 16–17% in 1861, and there was every evidence that this increase in sugar percentage might go on indefinitely. So selection became the fetish, the patron saint of the modern breeder of twenty-five years ago. Then came Professor Johannsen, of Copenhagen, in 1901 with his brown Princess beans. He, too, believed in the omnipotence of this method, and conceived the idea, from studying the work of Galton, that heredity might be controlled and made to accomplish desired objectives.

By constant breeding from the most desirable (plus) parents, more and more of the progeny would be of the desired type. In other words, the mean or average would be constantly shoved in the desired direction higher and higher. So Johannsen chose beans because they were self-fertilizing, prolific, and easily measurable to test this idea. But the results of his first progeny tests did not meet these expectations. From these results he concluded he was using mixed material, mixed material in the sense that beans of several distinct strains of one variety were

[1] Vilmorin, Jacques L. de. L'hérédité chez la betterave cultivée. Gauthier-Villars et Cie, Paris. 1923.

mechanically associated, just as one might bring together three or four sizes of shot, put them in a common receptacle and shake them. Whereupon he started a series of cultures from nineteen beans, each of which he carefully weighed and numbered. These 19 pure cultures or pure lines were selected in a plus or minus direction for six years, without any permanent or significant change in either direction. From these experiments, carried out in great detail, he concluded *that selection within pure lines was absolutely non-effective.* Such variations as did occur were environmental modifications. The means or averages of each line remained on the whole, the same.

Pure Lines.—Thus arose the technical conception of a pure line, which is quite different from what breeders had been used to calling pure-lines. In the latter case, the concept was based on somatic appearance or phenotypical characters. In the sense of Johannsen, a pure line is based on a genotypic analysis. A *pure line,* as defined by Johannsen, *is "the descendants from one single homozygotic organism, exclusively propagating by self-fertilization."* "A line ceases to be pure when hybridization or intercrossing disturbs the continuity of self-fertilization."[1] The apparent efficacy of selection that had been so commonly found or observed was simply isolation of pure lines from a mixed population, and once the line was isolated and "purified," the effect of selection ceased. This was a brilliant discovery, and has been largely accepted by geneticists as being in accord with their own observations and results. As easily seen from the definition of pure lines, which precludes bisexual inheritance, mixed populations must be the rule both in nature and in agriculture in general. A mixed population is a mixture of pure lines. The mixture may be either mechanical or due to intercrossing. An excellent illustration of the truth of the pure line concept is Vilmorin's wheat selections grown for 50 years without change (Fig. 685).

Systematic Relationships and Genetics.—It is a grave mistake to think as many do, that most of what constitutes the science of genetics has but slight application to solving the puzzles of the ancestral tree or trees, for life may have originated more than once. All phenomena are natural, and the fundamental laws

[1] Johannsen, W. The genotype conception of heredity. Amer. Nat. **45**: 129–159. 1911. p. cited 135.

and principles that result from the study of controlled cultures govern wild as well as cultivated plants, wild as well as tame animals.

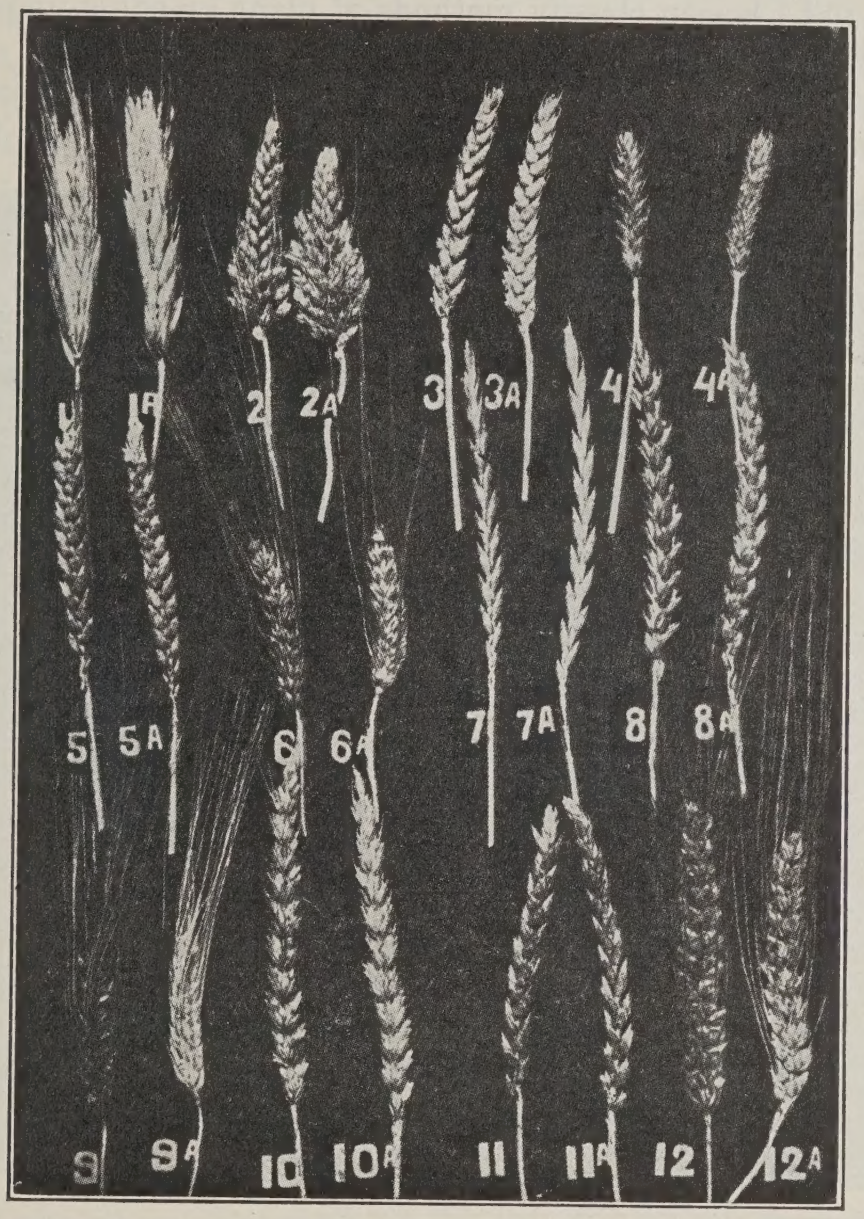


FIG. 685.—Fifty years of selection in wheat varieties by the Vilmorins. The illustration shows a typical head (unlettered numbers) of the variety when the selection work was started, and a typical head of the same variety (1*A*, 2*A*, etc.) after selection had continued for fifty years. Note the very close resemblance between the pairs of heads. (After A. L. and A. C. Hagedoorn.)

Applied Genetics or Practical Breeding.—This subject is strictly in the domain of a course in genetics and of necessity must be treated briefly here, but the student should realize its

practical importance in a definite, concrete fashion, as so much of genetic law and principle may seem far removed from the business of producing new varieties or improving old ones. Babcock and Clausen classify methods of plant breeding under the following four heads:

Mass selection—the method in use for centuries of picking out the best and largely employed today by farmers and gardeners

FIG. 686.—The original Concord grape vine and its originator, Ephraim W. Bull. (From an old print purchased in Concord, Mass.)

all over the world. Through this method such well known varieties of corn as Leaming, Reid Yellow Dent, and Boone County White were secured.

Line selection and progeny tests or the selection of a promising individual plant and the testing of its progency. This is the

method of many of the successful pioneer plant breeders of the 19th century, and is used at present very successfully at Svalöf, Sweden and at many experiment stations in the United States. Through its use many varieties of small grains, especially those particularly adapted to local conditions have been originated.

Hybridization followed by direct utilization or selection and the fixation of the new varieties—a very common method in use by the best breeders all over the civilized world, especially with ornamentals and vegetables propagated by seed.

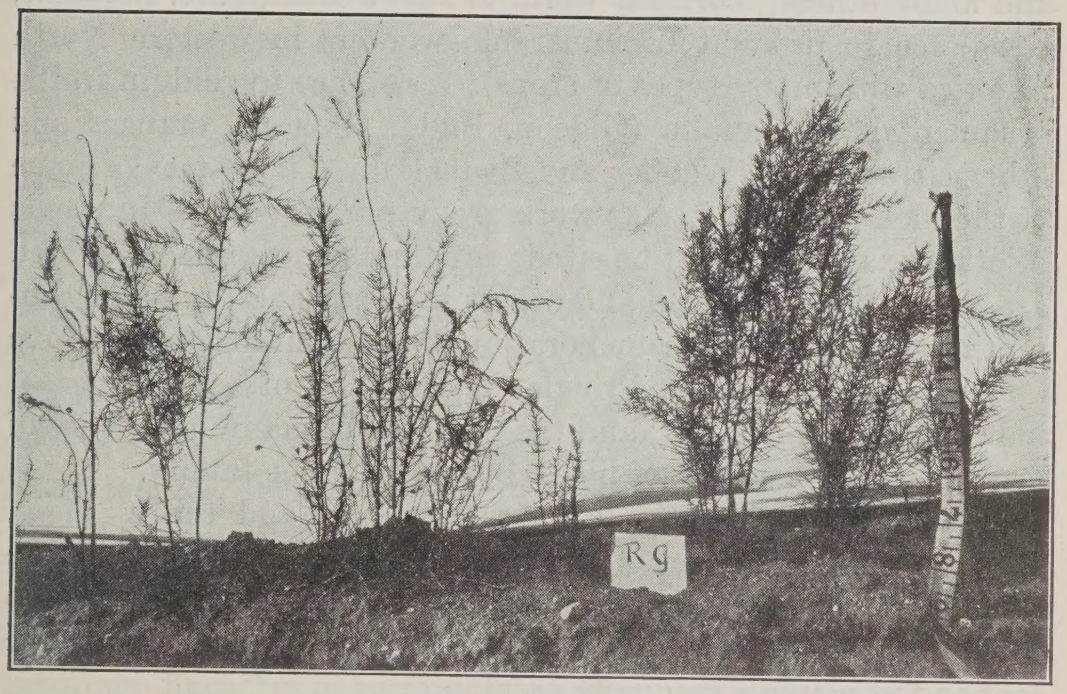


FIG. 687.—Breeding asparagus resistant to the rust disease. Mixed assortment of asparagus plants, those on the left not resistant to rust; those on the right resistant and healthy. (After Norton, U. S. Dept. Agric.)

Clonal or bud selection—in common use in securing new types of ornamentals and in keeping certain field and fruit crops free from deterioration, but limited in utility because of its relative rareness. The Washington or California navel orange is believed to have originated as a bud sport.

Through these methods, which involve the laws, principles, etc. briefly described in the preceding pages, new varieties of plants have been or are being originated for special purposes, such as resistance to various diseases [wilt in cowpeas, watermelon, cotton (Orton), stripe rust of wheat (Biffen), black rust

in wheat (Kanred variety of the Kansas Agricultural Experiment Station), various potato diseases, mildew in hops (Salmon) and gooseberries, bark disease or blister blight of chestnut (van Fleet), fire blight of pears (Kieffer, Reimer, Hansen), smut in oats, barley and sorghums (Reed, Barney, Gaines, Faris), wilt in flax (Bolley, Barker), rust in beans (Fromme), rust in asparagus (J. B. Norton), anthracnose in beans (Burkholder), yellows in cabbage (L. R. Jones)]; resistance to various insects [aphids of stone fruits (Beach), phylloxera of European grape (Rasmuson and many others), corn-ear worm of sweet corn (G. N. Collins)]; resistance to drought (innumerable workers in western North America with many types of crops); resistance to cold [in fruits, ornamentals and alfalfa (Gideon, Budd, Hansen), oranges and other citrus fruits (Webber and Swingle)]. The names of some of the men involved in this work are in parenthesis. Hundreds of other examples might be cited; outstanding examples of which are the work of Vilmorin and others in increasing the sugar content of sugar beets; the amelioration of the tomato from the love apple by Tilden, Hand, Pringle, Waring and others of the last half of the 19th century; and the breeding of many new types of ornamentals, especially of lilacs, by the Lemoine family.

Before the rediscovery of Mendel's laws and the building, through the last quarter of a century, of the great superstructure of modern genetics, breeders largely worked in the dark. So much labor was expended in repetition. The body of genetic fact and principle is gradually accumulating in sufficient quantity, so that some degree of prediction as to the outcome is possible, even before work toward the objective has begun.

CHAPTER XLIII

EVOLUTION

The Problem.—All science is largely occupied with the solving of problems. The phenomena of nature confront each one of us, but to the man of science they are all interrogation points—not to be merely observed and described, but to be interpreted and explained. Thus the great diversity of nature is a matter of common, every-day experience. We note the different kinds of birds and mammals, the various kinds of trees or of vegetables cultivated in our gardens; we know there are different races of men. Such knowledge has been universal from prehistoric times, but the significance of this fact of variety, and the desire to explain and understand it, were a late development in the intellectual advancement of the human race. Religion, art, and literature (especially poetry) were in advanced stages of development, before science, in the modern sense of the word, had more than begun to be. Thus the early attempts to solve the problem of diversity in nature were largely made before there had been perfected the method of modern science—the only method by which such problems can be attacked with any prospect of attaining correct solutions.

Alternative Solutions.—It is almost self-evident that there can be only two possible solutions of the problem of the present diversity; either things were made as they now are, or else the world, as made, has changed—is not now as it was formerly or originally. If it has changed then, again, there are two alternative explanations; either the change from one condition to another took place sporadically and by a series of "catastrophies" or sudden, large changes occurring within comparatively short periods of time; or the changes were gradual and orderly, and occurred throughout vast periods of time.

Fact and Inference.—If recorded history had begun with creation we would, of course, know which of these alternative explanations

is correct. One would only need to read the record of observed fact. But, in the absence of many of the facts, the missing data can be supplied only by inference. And here is where scientific method really begins. The earlier inferences were, for the most part, made too hastily, without sufficient knowledge of all the facts that might be known. Then, too, the inferences were not rigorously tested by further reference to known facts. If they seemed plausible, and if they agreed with preconceived notions—expecially with religious ideas, the inferences were soon accepted as correct, and very shortly all distinction was lost between the facts of observation, and the untested or hastily made inferences.

Scientific Method.—Recognition of the difference between fact and inference, and the development of a *reliable* method of arriving at *correct* inferences is one of the glories of the intellectual development of mankind, for it meant the discovery of the way to know the truth. No greater discovery than this has ever been made. It is called scientific method, not because its use is confined to the study of nature, but because it was largely developed in connection with the study of the various sciences. It is the method by which all knowledge is advanced, whether of the natural and physical sciences, or of history, language, theology, or any other subject.

Essentials of Scientific Method.—The essentials of scientific method are these.

1. *Open-mindedness.*—One must really want to know the truth, regardless of whether it will confirm his long-cherished ideas, or agree with his prejudices or wishes, or not. Lack of open-mindedness has been one of the greatest obstacles to the advancement of knowledge.

2. *Observation.*—All the facts possible that might bear directly or indirectly on the subject to be investigated, must be observed and recorded, carefully, accurately, thoroughly. Darwin and Wallace spent years recording thousands of facts.

3. *Comparison* of the facts. This is necessary in order to make the next step possible.

4. *Classification.*—This places our data before us in simplified form, facilitates clear thinking, and brings out relationships that might otherwise be overlooked.

5. *Generalization.*—This enables us to deal with groups or classes of facts, rather than with individual facts. We may, for example, discuss maple trees (or, better, the genus *Acer*), without having to refer to every maple we have observed and described.

6. *Drawing Inferences.*—Our first inference as to the probable explanation of the data we have gathered is called a *hypothesis.* Often several hypotheses are made. The essential point here is that the hypothesis must be thoroughly grounded on the observed facts; it must be such an inference as the facts suggest and fully justify. The hypothesis must be a *logical* inference from the facts. Herein is where a hypothesis differs from a mere guess—a guess being a hasty inference, commonly made with only slight reference to available facts. We may *guess* (or even believe) that the moon affects the weather, but a full knowledge of all facts bearing upon that question would never lead to a hypothesis to that effect.

7. *Testing the Hypothesis.*—If our hypothesis is correct it ought to enable us to make certain predictions as to other related facts; if it is true then certain other things will also be true. So the hypothesis is tested by being applied to additional facts. If we find it is not correct we must discard it and then frame and test another hypothesis, and so on until we find one that squares with the facts. This is the method of *multiple hypotheses* or of the *working hypothesis.* We work with it as if it were true until we find it must be abandoned. A hypothesis that has been thoroughly tested without being found at variance with the facts is called a *theory.* The *nebular hypothesis* of the origin of the solar system never became a theory, and is now definitely rejected by astronomers since it does not agree with many of the more recently discovered facts of astronomy. The *atomic theory* of Dalton, in chemistry, was first a hypothesis. It still holds as a theory though greatly modified from its original statement by Dalton.

Importance of a Knowledge of Method.—It is impossible to understand evolution or to discuss it intelligently unless one is familiar with scientific method as briefly outlined above. In fact, this knowledge is quite as important as a knowledge of the facts of nature, for the doctrine of evolution comprises hypotheses

and theories comprises advanced to explain the facts of nature that have been observed and recorded.

Hypothesis of Special Creation.—We noted above that there are two possible explanations of the diversity among living things, one being that things were created "in the beginning" as we find them now. When this hypothesis began to be rigorously tested by application to our increased knowledge of living and extinct plants and animals it was soon found hopelessly at variance with known facts. Not only have species of animals and plants become wholly extinct (*e.g.*, the carrier pigeon) or extinct in a state of nature (*e.g.*, the Ginkgo tree) within the period of recorded history, but a study of fossil plants and animals preserved in the rocks discloses the fact that many species that flourished in earlier geological ages are now extinct.

Furthermore, a study of fossils shows us that many, if not most, of the species of our present flora and fauna did not exist in earlier geological periods. Obviously they must have arisen since the time of any initial creation.

Evolution.—The study of living and fossil plants and animals discloses not only the fact that there has been a change in the species during geological time, but that the structure and behavior of organisms shows various degrees of relationship between certain groups which indicate a common ancestry. The facts are just as they would be if modern species had been derived by natural descent from species now extinct. The inheritance, however, has not resulted in monotonous repetition of characters, but gradual changes from generation to generation have finally produced a vast progeny quite unlike their probable ancestors, yet retaining certain characters that enable us to trace the ancestry.

Thus, for example, living and fossil cone-bearing trees have certain features, such as the bearing of cones, the microscopic structure of the wood, the number of leaves of the embryo in the seed, and others, which are difficult to explain except on the theory that the various species of conifers, living and fossil, have had a common ancestry. Such a mass of evidence has accumulated, all pointing to the same conclusion, that no one who is acquainted with this evidence at first hand now doubts the correctness of the conclusion. In fact, the idea of organic

evolution, the descent (with modification) of one species from another, has passed from the status of a hypothesis, to that of a thoroughly substantiated theory, and is, indeed, considered by most students of biology and other sciences to have passed from the realm of theory of that of demonstrated truth. In his much-quoted Toronto address before the American Association for the Advancement of Science, Professor Bateson,[1] while stating that we need more knowledge "as to the actual mode and processes of evolution," said: "Let us then proclaim in precise and unmistakable language that our faith in evolution is unshaken. Every available line of argument converges on this inevitable conclusion."

Similarly, Professor Frost, Director of the Yerkes Observatory, and one of the leading astronomers of the world, has stated in a recent pamphlet that "all the evidence points toward an orderly evolution of celestial bodies."[2] The evolution of one chemical element from another by means of radioactive transformations is now a matter of experimental demonstration.

Evolution vs. Transformation.—It is important that the fact of organic evolution be correctly conceived and stated. We must not think of one species of plant or animal as having been transformed into another, but of a later species as having been derived or descended from a pre-existing species. The latter may continue to exist; it is not transformed. The Concord grape, for example, was derived by descent (with modification) from the wild grape of New England, but the wild grape continues to flourish in its original habitats. The parental species, it is true, may eventually die out (as in the case of the five-toed horse, the progenitor of our modern two-toed horse), but not because it became transformed into a different species. Wild crab-apples were not transformed into our modern orchard apples; but the latter did evolve (descend with modification) from the former.

Biogenesis.—As stated above, organic evolution is an explanation of the existing diversity of species of plants and animals. The ultimate problem, of course, is the origin of life itself. What was the origin of the first plant or plants? This is a legitimate

[1] Bateson, William. Evolutionary faith and modern doubts. Science **55**: 55–61. Jan. 20, 1922.

[2] Frost, Edwin B. The heavens are telling. Am. Inst. Sacred Literature Chicago, September, 1924.

question, and several answers have been proposed. It has been suggested that life may have been brought to the earth from other planets. No biologist seriously entertains this suggestion, but even if it were true the answer to the question of the origin of life would be as far off as ever. The answer that life was "created by God" satisfies some minds, but does not constitute a scientific explanation, for the question of the scientific investigator is, *By what method* did God work? What were the various steps? For in science "explanation" means accurate, detailed description of the method by which a given result is accomplished.

Without attempting here to answer the question of the ultimate origin of life, we may say that one of the most fundamental generalizations of biological science is that there is now no life without antecedent life; living things come into existence only by one invariable and universal method, namely, as the offspring of preëxisting parents. This fact has become familiar in biological literature through its Latin statement, *Omne vivum e vivo*—All life from life. In all the study of biology no other method has ever been found by which any living thing comes into existence, and if we believe in the uniformity of nature (as we must do, else all science and in fact our daily lives would be impossible) then we must conclude that existing species have had pre-existing species as their parents. This is the essence of organic evolution. In all probability, conditions "in the beginning" must have favored the evolution of living matter (protoplasm) from non-living matter. With this primordial living matter organic evolution began.

Theories of Evolution.—But even if we consider that organic evolution is a fact, there still remains the difficult problem of discovering the *method* by which descent with modification has been brought about. It is not possible to discuss here all of the methods that have been suggested, from the time of the ancient Greeks until now; only two of them can be mentioned:

1. *Lamarck's Hypothesis.*—The noted French biologist, Lamarck (*Cf.* p. xiii), taught that animals became modified through the use and disuse of their various organs. For example, a certain animal, by reaching up for high foliage to eat, would cause his neck to grow longer. The increase in length would be inherited in the next generation, and by a repetition of this process in a

series of generations there would finally result an animal like a giraffe, with its long neck. To this hypothesis there are several objections. It applies only to animals, not to plants, and it takes for granted that "acquired characters" (the effects of use and disuse) are inherited from generation to generation. This

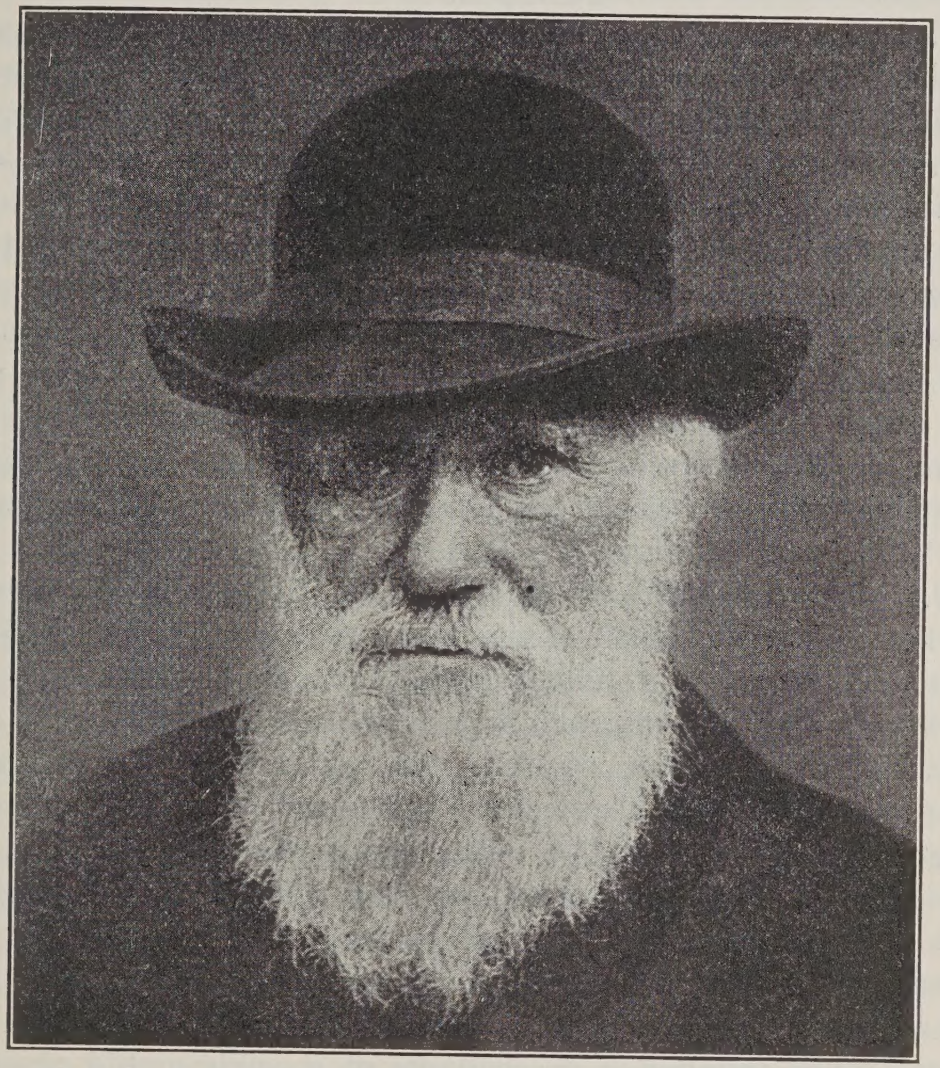


FIG. 688.—Charles Darwin. The publication of his "*Origin of Species*" in 1859, revolutionized human thought, and gave direction to all scientific and philosophic thinking from that time to the present.

has never been proved; in fact, the bulk of evidence is against that hypothesis.

2. *Darwin's Theory.*—As a result of twenty years of careful, first hand study of the facts of nature, Charles Darwin, reached the conclusion that the change in the kinds of species that inhabit the earth has been brought about by the operation of natural

causes, operating through long periods of time. The essential points in Darwin's theory are as follows:

a. Biogenesis.—Darwin did not attempt to explain the origin of life, but took for granted the existence of living organisms, and accepted as fact that all living things are produced only by descent from pre-existing parents.

b. Inheritance.—The characters of parents tend to reappear in their offspring in successive generations. Plants having flowers with five petals give rise to plants having flowers with five petals.

c. Variation.—Resemblance is seldom, if ever, perfect; offspring tend to vary from their parents either by loss of characters, the appearance of new characters, or by a quantitative variation of existing characters. A *moss-rose* may be the offspring of a smooth rose; a white strawberry may spring from a normal red-berried plant; normal sized barberry bushes may give rise to dwarf offspring (the box-barberry); Lamarck's Evening-primrose (*Oenothera Lamarckiana*) may give rise to the Giant Evening-primrose (*Oenothera gigas*), as it did in the garden of de Vries, in Amsterdam.

d. Fitness for Environment.—Some of the variant forms will be better fitted for their environment than others. Those best suited to their environment stand a much better chance of surviving and of producing offspring than do others.

e. Excessive Production.—The number of descendants of any plant or pair of animals would, if unchecked, eventually become so great that there would be neither room enough nor food enough for all. Among the slowest-breeding animals are elephants; one pair produces an average of only one baby elephant in ten years, yet Darwin calculated that if all that were born survived there would be 19,000,000 descendants of one pair in 740–750 years. The number of descendants of a single orchid plant or of a giant puff-ball in only ten or fifteen years would, if unchecked reach a number quite beyond comprehension (*Cf.* pp. 507 and 927).

f. Struggle for Existence.—Notwithstanding their enormous rate of reproduction the world is not crowded with either elephants, orchids, puff-balls, or any other species. Why? It was Darwin and Wallace who, independently, first raised this question and gave a satisfactory answer. The large number of

organisms in proportion to available food or space results in a *struggle for existence.* They struggle with each other often in direct combat (in the case of animals); or they struggle against the adverse conditions of environment. Thousands of dandelion seeds may fall on the same square foot of lawn. Obviously there is not room for a thousand plants. The seeds which germinate first or produce the most vigorous seedlings get the start of the others, crowd them out, and possess the ground. Darwin called this a struggle for existence, using the term, as he said, "in a large and metaphorical sense."

g. Survival of the Fittest.—Darwin called those plants and animals best suited to succeed in their environment the fittest, and these succeed where the others fail. Wolves attack a flock of sheep; some of them attempt to run away. One or two of the sheep may be endowed with more acute senses than the others and detect the approach of the wolves before the others do. They begin sooner to run away. If any survive it will be those possessed of the keenest senses, or those that can run fastest; or, as Darwin said, it is the fittest that survive.

Herbert Spencer regarded struggle and survival from the standpoint of nature; the result was as if nature had selected the best to survive, and so Spencer called the process one of *natural selection.* More recently it has been suggested that while plant and animal breeders *select*, nature really *rejects* the unfit, so that *natural rejection* would be the better term. The idea is essentially the same whichever terminology we employ.

"Evolution" Not Synonymous with the "Origin of Species." The conception of evolution is applied, not only to explain the history and present condition of the plant and animal kingdoms, but to explain the origin, history, and present condition of the solar system, the earth on which we live, the chemical elements and compounds, the development of languages, of religions, of political ideas, of human society, government, and morals. In fact, evolution postulates that whatever is, in the realm of matter or of ideas, is the result of gradual change, operating throughout long periods of time, strictly in accordance with natural law. The evolution of organisms is called *organic evolution.* The origin of species is only a part of organic evolution; we must, for example, also explain the origin of genera, of the plant

families, of the two kingdoms (the animal, and the plant); and, ultimately, of life itself.

"Darwinism" and "Evolution" Not Synonymous.—From the preceding discussion we learn that Darwinism is only one of several methods that have been proposed to explain the origin of species. It is one of several theories of organic evolution. It should be kept clearly in mind that, while practically all biologists consider evolution as a fact (as the actual method by which the present condition of the universe has been attained), Darwinism has always been recognized, first as a hypothesis, then as a theory.[1]

Present Status of Darwinism.—Like practically every scientific hypothesis or theory, Darwinism, as originally stated by Darwin, has been modified or restated in the light of biological discoveries made since Darwin. For example, it is recognized that Natural Selection does not *cause* the new features that characterize new species. It operates only as a sieve, letting through the fittest, and screening out the unfit—those not able to survive and reproduce in competition with others. Darwin, moreover, was in doubt as to the method of origin of the fittest. Investigations during the past thirty years have thrown a flood of light on this question. A full discussion of the question of the present status of Darwinism belongs more properly to advanced courses, but it should be kept in mind that Darwinism is not a fetish that is worshipped in the temple of science. It has been one of the most fruitful working hypotheses ever proposed, stimulating investigation and pointing the way to further research, to a better understanding of nature, and even to its own modification. If new facts should seem, in time, to necessitate the complete abandonment of Darwinism, the scientist will be the first to welcome those facts (just as he will be the first to discover them), and will gladly discard his worn-out tool (Darwinism) in favor of a newer and better one, just as he discarded the hypothesis

[1] The importance of keeping this distinction clear (*i.e.*, between fact and theory) has recently (1925) been emphasized by attempts to show that there is an essential antagonism between evolution and religion. In the popular discussions of the question evolution has been commonly, but erroneously, referred to (though not by biologists) as synonymous with Darwinism, and the theory of Darwinism has been erroneously referred to as a "fact."

of a flat earth in geology, and the nebular hypothesis in astronomy; and just as he has been eager to modify the atomic theory in chemistry, and may (in the light of recent discoveries) have to discard or at least modify the wave theory of light, and the Newtonian conception of gravitation. All that the scientific man asks is that the evidence shall amply justify this revision or rejection of old ideas.

Origin of the Fittest.—New characters in plants and animals may originate either by crossing one kind with another, or by variation in the germ plasm (*chromatin*) apart from crossing. Darwin recognized two kinds of variations, but was uncertain which was more important for his theory. He inclined to consider *fluctuating variations* (which we now understand are the result of change in the environment, without any fundamental change in the germ-plasm) as the material upon which natural selection worked.

Fluctuating variations are quantitative variations about a mean. For example, in a field of corn there may be all degrees of height, some very short, some very tall, some of average height, due only to differences in environment. But in successive crops the mean (*i.e.*, the average of the extremes) remains the same.

The work of de Vries, the celebrated Dutch botanist, emphasized another kind of variation known as discontinuous or saltative variation or, as de Vries called it *Mutation*. Mutations are due to a fundamental change in the germ-plasm—that is, to a change in the genotypical constitution of the germ-cells, not the result of segregation, crossing over, or recombination of genes. By mutation there arises a new mean, about which the character under consideration fluctuates, even though the environment remains essentially the same. (*Cf.* p. 962 *et seq.*)

The difference between the two kinds of variation is simply illustrated by the simile of the pendulum. The swing of the pendulum through its arc represents fluctuation or fluctuating variation; the center point of the arc is the mean. If, then, something causes the pendulum to swing from a new point, a change comparable to a mutation has taken place. The pendulum then fluctuates about a new mean.

According to recent biological researches, the heritable variations caused either by crossing or by mutation are the material

on which natural selection operates. This is the essential point of what de Vries has called *the mutation theory.* The theory was not proposed as a substitute for natural selection; it sought to point out the nature and origin of the fittest. On this point Darwin had been uncertain.

Evolution and Religion.—It is the province of science to describe the universe as accurately as possible. When the scientific man says he has *explained* something he means only that he has described it accurately and minutely; he understands it better only in the sense that he knows it more thoroughly. There still remains the great mystery of the cause of all things. With this, natural science has nothing to do; that is the province of philosophy. The stages through which our earth has passed from the beginning until now form a record which may be more or less imperfectly interpreted by the geologist; the record is the same whether we say "God made it," or not. Science does not profess to pass on this question. Darwin, in his "*Origin of Species*," speaks of a creator (*Cf.* p. 915). Many scientific men are devoutly religious.

In some of our large bakeries the ingredients, say of crackers, are taken to the top floor where they are mixed together by machinery. On their way down to the delivery door on the ground floor, they are successively baked, placed in boxes, the covers nailed on, the labels affixed, and the box addressed to some retail store—all by machinery—"not touched by human hands," as the advertisements say. A visitor to the factory could observe and accurately describe all these processes without any reference to a mind, or an inventor or "prime mover" behind it all. What he sees *suggests* that the bakery does not run itself,[1] but the object of the visitor is to describe what he sees. This is the function of science—to describe (and interpret) the universe; as to what is back of it all—that is the function of philosophy and theology. Any "conflict" between science and theology means that they do not understand each other, for there can be no conflict between two truths. That science and theology should remain in wilful ignorance of each other's aims, methods, and results, that is immoral and inexcusable.

[1] Professor Frost, in the pamphlet cited on page 1005, says: "There is no adequate evidence known to the writer that the universe is automatic, that it has within itself the power to make the laws which govern it. Mere matter cannot be imagined to be endowed with such capacity."

INDEX

Aaronsohn, Aaron, 814
Abiogenesis, 196
Abscission layer, 102, 138
Absorption, organs of, 32
Abutilon, 182, 391, 665, 668
savitzii, **183**
Acacia, **976**
false, 628
Acacia melanoxylon, 58
sphaerocephala, 205
Acanthopanax pentaphyllum, 707
Acer Pseudo-Platanus, **794**
saccharum, 657
Aceraceae, 657
Achene, 407
Achras Sapota, 723
Aconite, Winter, 336
Aconitum, 392, 596
Acorus Calamus, 875
Acquired characters, 945, 1007
Adder's Tongue, Yellow, 887
Adhesion, 566
Adiantum, **415**
concinnum, **417**
Aecidia, 483
Aecidium berberidis, 480
Aeciospore, **484**
Aecium, 483, **485**
Aegilops, 807
Aeranthus, 921
Aerobes, 147
Aesculus glabra, 658
Hippocastanum, 251, 658
Buds of, **251**
Pavia, 658
After-ripening, 760
Agapanthus umbellatus, **794**
Agar-agar, 447
Agaricaceae, 479
Agaricus arvensis, **506**
campestris, **501, 505, 512**
var. columbia, **512**
Agave, **100**, 334, **897**
americana, 896
atrovirens, 897
decipens, 898
rigida var. *Sisalana*, 897
sisalana, 897, **898**
Victoria-Reginae, **100**
Agropyron, 797
repens, 798
Agrostemma, 591
Agrostideae, 819
Agrostis, 800
stolonifera, 731
Ailanthus Family, 655
Air in houses, effect of plants on, 155
Air-chamber, 58
Air-root of an orchid, **919**
Aiton, William, 586
Albinos, 963
Albugo candida, 520
Albuminous, 353
Alcoholase, 137
Alder, Black, 657
Alders, 587
Ale, "Ginger," 745
Aletia argillacea, 675
Aletris, 887
Aleurone, 192, 811
grains, **191**
layer, **813**
Alfalfa, **162, 629**
leaf-spot, 523,
Roots of, 111
Yellow-flowered, **327**
Alga, Red, 447
Algae, 447

Algae, Blue-green, **459**
Brown, 448
classification of, 448
Red, 448, **449**
Alinit, 242
Alisma Plantago-aquatica, **797**
Alismaceae, 796
Allelomorphic, 952
Allelomorphs, 952, 960
Multiple, 982, 986
Allium ascalonicum, 882
canadense, 882
Cepa, 324, **881, 882**
var. *bulbellifera*, 882
var. *multiplans*, 882
Allium cernuum, 882
sativum, 882
Schoenoprasum, 882
tricoccum, 882
vinelae, 882
Allspice, 694, **695**
Almonds, 627
Alnus, 587
Aloe, 887
distans, 100
Aloe, American, 896
Alsike clover, 358
Altenberg, 967
Alternaria Solani, 463, 769
Althaea, 665, 668
Alveolus, 841
Alyssum maritimum, 608
Amanita muscaria, **504**
phalloides, 501, **502**
Amarantaceae, 588, 590
Amaranths, 588
Amaryllidaceae, 895
Amaryllis, 895
Amaryllis Family, 895
Ambrosia, 207
Ambrosia artemisifolia, 791
Ambrosia beetles, 206
trifida, **791**
Ambrosiaceae, 791
Amelanchier, 619
Ament, 339
American Spikenard, 705
Ammonia, crop-plants that use, 230
production of, 226
Amomum Cardamon, 909
Ampelopsis, 664
Amphitropous, **345**
Amygdalin, 627
Amygdalus communis, 627
Amylase, 139
Amyloplasts, **181**
Amylum, 139
Anacardiaceae, 656
Anacardium occidentale, **657**
Anaerobes, 141, 147
Anagallis, 357, 720
Analogous, 436
Analogy, 922
Analysis of plant substance, rough, 29
Ananas sativus, **879, 880**
Anaphase, 22, **23**
Anaphylaxis, 403
Anatomy, external, 14
Anatropous, **345**
Andreaeales, 440
Androecium, 350
Andropogon Helepensis, 824, 830
sorghum sudanensis, **825**, 830
Andropogoneae, 824, 831
Androspores, 550
Anemone, 347, 595
coronaria, 330
Anemone, Poppy, **330**
Anemonella thalictroides, **348**
Anemophilometer, 402
Anemophilous, 381
Angraecum maculatum, **923, 924**
sesquipedale (Orchid), **388**, 392
Animals parasitic on plants, 218, 219
Annuals, 333
Annulus, 411
Anona Cherimolia, 594
Muricata, 594
Squamosa, **594**
Anthemis, 791
Anther, 346
Antheridia, 412, **416**
Antheridiophores, **445**, 446

Anthesis, 7, 358, 819
Anthurium, 337, 875
Anthoceros, 218
Anthonomus grandis, 676
Antirrhinoideae, 774
Antirrhinum, 774, 979
Apetalae, 571
Apium, 708
Aponogeton fenestralis, **379**
Apothecia, **210**
Apple, 619, **620**, 970
development of the, **359**
Apple Family, 618
Apple Trees, 165
Apples, Chimera in, **989**
fruit spot of, 463
Aquifoliaceae, 657
Aquilegia, 596
Araceae, 875
Arachis hypogea, 359, **360, 630**
Arales, 875
Aralia hispida, 707
nudicaulis, 705
racemosa, 705, 707
spinosa, **56**, 707
Araliaceae, 705
Aranthe elongata, **75**
Arbutus, Trailing, **715**
Archegonia, 413, 415
Archegoniophores, **445**, 446
Archichlamydeae, 571
Arctium, 791, **792**
Arctostaphylos, 334
Arenaria, 591
Arenga saccharifer, 855
Aril, **356**
Arisaema triphyllum, **872**, 875
Aronia, 619
Arrow-arum, 875
Arrowgrass Family, 796
Arrowhead, **342**, 796
Arrowroot, 902, 909
West Indian, 911
Artichoke, Jerusalem, 791
Arum Family, 875
Arundinarieae, 803
Asci, reproduction by, 472
Asclepias, **356, 390**
Ascocarp, 474, **476**
Ascolichen, 210
Ascomycetes, 463
diseases caused by, 521
Ascophyllum nodosum, 450, **451, 452, 453**
Ascospores, 461, **473**
Ascus, 461, 473
Ash, 726
Bud scales of, **251**
Asimina triloba, 594
Asparagus, 940, 946, 999
Garden, **889, 890**
Asparagus asparagoides, 891, 893
medeoloides, 890, 891, 893
officinalis, **889, 890**
plumosus, **891**
sprengeri, 891
Asparagus-fern, **891**
Aspidistra, 391
Aspirin, 586
Assimilation, 195
Aster, 791
Asthma, Bronchial, 405
Aucuba japonica, 334
Availability, 166
Avena fatua, 66
strigosa, **805**
Aveneae, 817
Avicenna, **701**
Avocado, 375, **603**
Awn, **818**
Azalea, **713**, 963
Flame, 714
lutea, 714
Mountain, 714
nudiflora, 714
viscosa, 714
Azotobacter, 211
vinelandii, **239**

Babcock, 960, 994
Bacillus amylovorus, 536
dentrificans, 232
ellenbachiensis, 242
mesentericus vulgatus, 226

Bacillus mycoides, 226
phytophthorus, 769
radicicola, **234**, 235
root-tubercle, **234**
Solanacearum, 769
subtilis, 226
typhosus, 537
Bacteria, 534
Ammonifying, **226**
and the dairy, 544
and plant diseases, 535
forms of, **516**
helpful, 544
Nitrite, 228
Nitrogen-fixation by Molds and, 237
Bacterium fluorescens, 232
savastanoi, 727
Balsam of vanilla, 931
Balsa wood, 587
Bamboo, Giant, 802
Male, 803
Spiny, 803
Spring, 802
Water, 823
Bamboo Manna, 805, 806
Bamboos, 802
Bambusa arundinaceae, 802, 803
Bambuseae, 802
Banana, **55**
Red, 906
Bananas, 902, **903, 904, 905**
Banks, Sir Joseph, 599
Banyan, **578**
Baptisia australis, **344**
Barberry, 388
Box, 1008
Barberry Family, 602
Bark, structure of, 264
Barley, 66, **191**, 391, **799**, 816, **817**, 969, 1000
covered smut of, **496**
types of, **817**
Barney, 1000
Barnyard grass, 797
Basidia, 483
Basidiolichen, 210
Basidiomycetes, 463, 479
Basidiospore, 483, 503
Basidium, 503
and spores, development of, **510**
Basil, Sweet, 741
Basswood, 665
Bast fibers, 72
Bateson, 976, 977, 1005
Batrachium, 379
Bats, 391
Battata Virginiana, 747
Bauhin, Gaspard, 562
Bauhinia anguina, 803
Baur, 975, 991
Bayberry, 586
Bayonet, Spanish, 887
Beach, 1000
Beach Plum, 627
Beal, 983
Bean, **254**, 356, 979
Broad, 628
Castor oil, **938**, 992
Hyacinth, 632
Kidney, **387**, 628
Scarlet-runner, 387, 392
Bearberry, 334
Beard-tongue, 775
Bearing, alternate, 623
annual, 626
Bed-straws, 776
Bee hives, 397
Beech drops, **201**
false, 719
Beechnut, 587
Bee-tree, 665
Beet, **588**
Beggiatoa, 184
Begonia metallica, **294**
Begonia, Rex, **311, 341**
Begoniaceae, 679
Begonias, 679
Bellflower, **789**
Family, 788
Belling, 966
Benincasa cerifera, 112
Bent Grasses, Creeping, 731

Bent grasses, 800
Benzoin, 602
aestivale, 604
Berberidaceae, 602
Berberis, 388
Berry, 407
Beta maritima, 590
patula, 590
vulgaris, **588**
vulgaris Cicla, 588, **589**
vulgaris cruenta, 589
Betula, 587
alba, **261**
lutea, **263**
populifolia, **151**
Betulaceae, 587
Bidens, 791
Biennial habit, 108
Biennials, 190, 333
Biffen, 999
Bignoniaceae, 775
Billbergia, 99
thyrsoides, **101**
Bindweed, 732
Binominals, 563
Biogenesis, 196, 1005, 1008
Birch Family, 587
Birch, White, **151**
Yellow, **263**
Birches, 587
Bird Cherry, 627
Bird's-nest Orchid, 923
Bittersweet, **771**
Climbing, 657
Blackberries, 615
Blackberry, Wild, **359**
Black-eyed Susan, 791
Blackhead cranberry worm, 719
Blackhead fire worm, 719
Blackleg, 769
Bladderwort, 194
Blakeslee, 966
Blastophaga grossorium, 580
Bleeding, 76
Bleeding-heart, 606
Blister-blight, 520
Blister-rust, White pine, **528**
Bloodroot, 605
Bloodwort Family, 895
Blue Cohosh, 602
Blue Flag, 898
Blue Gum, 695, 699
Blue-Bells-of-Scotland, 788
Blueberry, **368,** 716
High-bush, 369
Blue-eyed-Grass, 898
Bluegrass, 799
English, 385
Bock, Hieronymus, 562, 922
Bog, 711
Boneset, 791
Bordeaux mixture, 67
Botany, 3
systematic, 557
Bouncing Bet, 591
Bouvardia, 782
Box Family, 656
Box-barberry, 1008
Boxwood, 656
Bracteole, 336
Bractlet, 336
Bracts, 336
flower, 839
Branches, innovation, **442**
origin of, 266
Brasenia, 593
Brassica alba, **278**, **279**, 609
campestris napo-brassica, 608
chinensis, 608
napiformis, 608
Napus, 609
nigra, **606**, 609
oleracea capitata, 608
oleracea caulo-rapa, 608
oleracea gemmifera, 609
Pe-tsai, 608
Rapa, 608
Bread, entire wheat, 813
graham, 813
unleavened, 134
whole wheat, 813
Bread-from-heaven, 213
Bread-mold, **462**
Break, 978

Breaking, 637
Breathing, 150
Breeders, 885
Breeding, applied genetics or practical, 997
Breeding true, 937
Brefeld, 135
Bridge-grafting, 314, 315, **316**
Bridges, 966, 994
Brink, 974
Broccolli, **607**
Bromeliaceae, 879
Brood-buds, 305
Broom corn, 826, 828, **829, 831**
Bromeliads, **204**
Broussonetia, 577
Brown, Robert, **16**
Brown rot of peach and plum, 521
Brunella vulgaris, 740
Brünn, Augustinian cloister at, **950**
Brussels sprouts, 609
Bryonia, 979
Bryony, Black, 794
Bryophyllum crenatum, **328**
Buckeye, Ohio, 658
  Red, 658
Buckthorns, 658
Buckwheat, **346, 584**
Budd, 1000
Budding, 136, 305, 316
Bud-formation, 105
Buds, 324
  axillary, **266**
  horse-chestnut, **251**
  inhibiting effect of apical, **763**
  supernumerary, 267
Bud-scales, 105
Bud-scales of an ash, **251**
Bud-sport, **965**
Buffalo grass, **34**
Bulb, broken, 885
  scaly, **324**
  tunicate, 323, **324**
Bulbils, 323, 326
Bulblets, **324,** 882
Bulbocodium, 895
Bulbs, 323
Bull, Ephraim W., **998**
Bull's-horn Thorn, 205
Bully-tree, 723
Bundle, dictyledonous, 72
  fibro-vascular, 69
  monocotyledonous, 71
  open, 72
  radial, **75**
  vascular, **73**
Bundle-sheath, 75, **76**
Bunt, **491, 492, 494**
Burdocks, 791, **792**
Burkholder, 1000
Burning Bush, 657
Bur-reeds, 796
Burrill, Thomas Jonathan, 536
Butter, Cacao, 667
Butter, Cocoa, 667
Butter-and-eggs, **774**
Buttercup, 347, **348**
  water, 379
Butternut, 587
Butterworts, **355,** 794
Button-bush, 776
Buxaceae, 656

Cabbage, **607,** 608, 939, 944
  Chinese, 608
  Wild, **607**
Cabomba, 592
Cactus, **220**
Cactus, Giant, **95**
Caesalpinaceae, 627
Caesalpinoideae, 627
Caffein, 686
Cajanus, 633
Cala Lily, 337, 875
Caladium esculentum, 876
Calamus, 856
Calamus Root, 875
Calanthe Dominii, 922
Calcutta, Black Hole of, 156
Calisaya Bark, 780
Calla palustris, **283,** 391, **873,** 875
Calluna vulgaris, **712**
Calochortus, 887
Calorimeter, 150

Calyptra, 440, **696,** 697
Calyx, 7, 350
Camassia, 887
Cambium, 72
interfascicular, 72, **259**
Camerarius, Rudolph Jacob, **364**
Camomile, 791
Campanula, **789**
Erinus, 788
Medium, 788
rotundifolia, 788
Campanulaceae, 788
Campulales, 788
Camphor, 604
Camphora officinarum, 604
Campion, 591
Camptosorus rhizophyllus, **329,** 331
Campylotropous, 345
Canada Lily, **324**
Cancer-root, **215**
Candytuft, 608
Cane, small, 798
Canna, **910,** 965
Canna Family, 910
Cannabinaceae, 582
Cannabis sativa, **582**
Cannaceae, 910
Canoe-birch, **261**
Cantaloupes, 784
Canterbury Bells, 788
Caoutchouc, 639
Capers, 606
Capparidaceae, 606
Capparis spinosa, 606
Caprifigs, **579,** 580, 581
Capsella Bursa-pastoris, 608
Capsicum annum, 745
Capsule, 407
Carbohydrates, 159
manufacture of, 178
Carbon cycle, **154**
Carbon Dioxide, source of, 175
Cardamon seed, 909
Cardinal Flower, 789
Cardiospermum Halicacabum, 658
Carduus, 791
Carica Papaya, 686, **687, 688**
Caricaceae, 686
Carnation, 591
pollen of, 386
Carnegia gigantea, **95**
Carpelodes, **601**
Carpels, Petalody of the, 347
Carpinus, 587
Carpogonium, **473**
Carpospores, 461
Carpotropism, 288, **289**
Carrion-flower, 892, **893**
Carrion-fungi, 479
Carrot, 709
Caruncle, 357
Carya, 587
Caryophillaceae, 588, 591
Caryophyllus aromaticus, 692
Caryopsis, 803, 821, 841
Caryota Urens, 856
Cashew Family, 656
Cashew nut, **657**
Casimiroa edulis, 721
Cassava, Bitter, 644
Sweet, 644
Cassia bark, 605
Cassia marilandica, 628
Tamala, 605
zeylanicum, 605
Cassiawood, 605
Castalia, **356**
Castanea, 587
Castilla elastica, **642, 643**
Castilloa elastica, 643
Castor bean, 979, 983
Castor-oil, **72**
Castor-oil plant, **254,** 638
Casuarinales, 571
Catalpa bignonioides, **775**
Catalpa, Umbrella, 313
Catalysis, 140
Catchfly, 591
Catkin, 339
Catnip, **740**
Cat-tail Family, 796
Cat-tail grass, 819
Cat-tails, **795**
Cattleya, **207,** 925, 927

Cattleya crispa, 916
fertilization of, 915
Trianae, **913**
Cauliflower, **607**
Caulophyllum thalictroides, 602
Cavity, germination, 682
Cecidomyia oxycoccana, 719
Cedar, West Indian, 655
Cedrela odorata, 655
sinensis, 655
Toona, 655
Celandine, 605
Celastrus scandens, 657
Celastraceae, 657
Celeriac, 708
Cell, 15
Cell-division, 22
Cell-plate, 459
Cell-sap, 18
Cells, Antipodal, 354, 849
companion, 71
number of, in a plant, 24
Cell-wall, **15**
Celtis, 576
Centaurea, 791
Centradenia floribunda, **381**
Centripetal, 7
Century Plant, 334, 896, **897**
Cephalanthus, 776
Cerastium, 591
Cereals, 945
Cereus giganteus, **95**
Ceriman, **874**
Cetraria islandica, 213
Chaenomeles, 626
Chaff, 337
Chalaza, 352
Chalazogamy, 352
Characters, acquired, 945
new, 966
pea, **952**
Chard, Swiss, 588, **589**
Chayote, 788
Cheese, ripening of, 477
Cheiranthus cheiri, 386, 608
Chelidonium, 944
majus, 605
Chelone, 775
Chemical infinitesimals, action of, 167
integration of, 169
Chemosynthesis, 184
Chemotropism, 272
Chenopodiaceae, 588
Chenopodiales, 587
Cherimoya, 594
Cherry, European bird, **326**
perfumed, 627
Chestnut, 587, 1000
water, **355**
Chestnut blight, **522, 523, 524**
Chickweed, Mouse-ear, 591
Chicle, 723
Chicory, **790**
Chimeras, 988, **990**
Chimeras, Tomato-nightshade, **990**
Chives, 882
Chlamydospore, 461
Chlorophyll, necessity for, 199
Chlorophytum elatum, **320**
Chloroplasts, **14,** 16
Choanephora, **469**
Chocolate, **666,** 667
Choke Cherry, 627
Chokeberry, 619
Chondriosomes, **15,** 20
Chondrus crispus, 447
Choripetalae, 571
Christmas fern, **411**
Chromatin, 20
Chromatophores, 456
Chromomeres, 981
Chromosomes, **22,** 960, 971
and genes, **975**
homologous, **978**
mapping the, 981
number of, 966, 972
Chrysanthemum, 940, 963, 970
Chrysanthemum leucanthemum, 791
Chrysosplenium, 612
Cichorium Endivia, 790
Cichorium Intybus, 789, **790**
Cider and vinegar, 626
Cilia, 414

Cinchona, 777, **780**, 781
officinalis, **779**
Cinchona bark, 779
Cinchonidine, 781
Cinchonine, 781
Cinnamomium Camphora, 604
Cassia, 605
glanduliferum, 605
iners, 605
zeylanicum, **604**, 605
Cinnamon, **604**, 605
Cinnamon Vine, 894
Circummutation, 256
Cissus laciniata, **220**
Cistaceae, 679
Citron, 784
Citrulus vulgaris, 784
Citrus, 645
aurantifolia, 654
Aurantium, 644
aurantium sinensis, 650
bergamia, 649
decumana, 653
grandis, **652**, 653
ichangensis, 652
japonica, 651
limetta, 654
Limonia, 653
Medica, 651
mitis, 653
nobilis, 650
trifoliata, 647, 648
species and varieties of, 649
Cladonia, **210**
rangiferina, 213
Classes, 560
Classification and evolution, 564
natural versus artificial, 561
need of, 557
Clausen, 960, 994
Clavariaceae, 479
Claviceps purpurea, **521**
Claws, **799**
Clearweed, 584
Cleft grafting, **990**
Cleistogamy, 391
Clematis, 595
Clerodendron, **374**
Clethra, 719
Clethraceae, 719
Climate, 124
Climbing, 257
Clinandrium, **912**
Clinostat, 787
Clintonia, 891
Clostridium pasteurianum, **239**
Clove, **693**
Clover, 4
Red, 109
Cloves, 692
oil of, 694
Club-root, **515**
Clusia, **206**
Clusius, Carolus, 750
Coalescence of petals, **348**
Cocaceae, 862
Coconut, **860, 861, 862**
Coconut-oil, 860
Coconuts, germinating, 861
transportation of, 862
Cocos nucifera, **857, 858, 859**
Coenocyte, 461, 455
Coffea arabia, 776, **778, 779**
flowers of, **779**
Coffee, 776
leaves of, **779**
Coffee-tree, Kentucky, 628, **778**
Cohesion, 566
Cola acuminata, 667
Cold storage, 553
Coleoptile, **355**, 812, **813, 852**
Coleorhiza, 812, **852**
Colic-root, 887
Collateral, 72
Collins, 984, 1000
Colloids, 17, 50, 139
Colocasia, 62, 876
antiquorum, 50
Colpothrinax Wrightii, **276, 855**
Columbine, 596
Columella, 442, 467
Column, **916**
Colza, 606
Coma, **356**, 357

Comatricha suksdorfi, **515**
Commelina, 879
Commelinaceae, 879
Commensalism, 205
Compass plants, 112, **113**
Compositae, 789
Composite family, 789
Conceptacles, 451
Concord grape, **998**
Cone, Carpellate, **429**
Cone-flower, 791
Conidia, 461, **473, 476**
Conidiophores, **476**
Conidiospores 461, **473**
Conjugation, 19, **456, 457**
Connective, 681
Conopholis americana, **215**
Conservation of forests, 121
Constitution, factorial, 960
Convallaria, 892
Convallariaceae, 889
Convolvulaceae, 731, 992
Convolvulus arvensis, 732
Copper, in plants, 164
  toxic to green algae, 164, 448
Coprinus comatus, **518**
  lagopus, 549
Coptis, 595
Corallorhiza, 215
Coral-root, 215
Corchorus, 665
Core of an apple, **619**
Coreopsis, 791, **792**
Cork, 264
  layers of growth, **263**
Cork-cambium, 262
Cork-oak, 263
Corm of Cyclamen, **324**
  of Crocus, **324**
Corms, 323
Corn, **37, 38, 231, 367, 382, 984,** 969, 998
  Broom, 828, **829,** 831
  field of Indian, **837**
  grain, **852, 853**
  grain, endosperm of, 853
  Hogue's Yellow Dent, **370, 371**
Corn, Indian, **71,** 832
  pod, 839
  prop roots of Indian, **836**
  smut, 498, **499**
  what is an ear of, 846
Cornaceae, 705
Corn-border, European, 219
Corn-cockle, 591
Corn-ear worm, 675
Corn-starch, 854
Cornus canadensis, 337
  florida, **335,** 337, 965
Corolla, 7, 350
Correlation, 288, **290**
  importance of, 296
Correns, Carl E., **948**
Cortex, 72
  secondary, 262
Corticium vagum, 769
  var. *Solani*, **519**
Cortinarius cinnamomeus, **503**
Corydalis aurea, **356**
Corylus, 587
Corymb, **337,** 339
Corypha umbraculifera, 803
Cotoneaster, 619
Cotton, 391, 665, **668, 673,** 999
  deterioration of, 398
  diseases of, 675
  field, 670
  flower of, **673**
  selective pollination of, 399
Cotton-boll, 674
  weevil, **676, 677**
  worm, 675
Cotyledon, 70
  rudimentary, **355**
Cotyledon agavoides, **100**
  Hovei, **100**
Cotyledons, 10, 11
Couch grass, 797
Coupling, 977
Cowpeas, 632
Cowslip, 720
Crab grass, 798
Cranberries, 716, 717
  harvesting, **718**

Cranberry, High-bush, 719
Cranberry rootworm, 719
Cranebills, 634
Crassulaceae, 611
Crataegus, 619
Creation, hypothesis of special, 1004
Crepis, 966
virens, **973**
Cress, Garden, 608
Crinum Americanum, 895
Crocus, 901
vernus, 900
Cronartium pyriforme, 529
ribiocola, 528
Cropping, loss of nitrogen by, 223
Crops, drought-resistant, 124
Crossing, 366, 961
limits of, 991
variation due to, 947
Crossing-over, 975, 977
Crossing-over, generalizations on, 978
Cross-over, double, 979
Cross-overs, 977
Cross-pollination, 847, 951
agents of, 378
economic bearings of, 366
effect of, on yield, 368
how insured, 373
types of, 366
Crowfoot Family, 595
Crown-galls, **536**
Crown-imperial, 390, 887
Cruciferae, 606
Crystalloid, 17, 50
Cubeb, **574**
Cucumber, **783,** 784
Sikkim, 786
Cucumber-root, Indian, 892
Cucumis anguria, 784
Hardwickii, 786
sativus, **783,** 784
Cucurbita maxima, 784, **785**
moschata, 783
Pepo, 783, **784**
Cucurbitaceae, 783
Cucurbitales, 782
Cup-fungus, **478**
Curcuma angustifolia, 909
leucorrhiza, 909
Currant, Mackerel, 613
Currants, 612, 663
Red, **613**
Cuscuta, **216, 217, 218,** 732
Cuticle, 62, 821
Cuttings, **309**
Cyanophyceae, 459
Cycadaceae, 211
Cycas normanbyana, a stoma of, **115**
revoluta, **212**
Cydonia japonica, 626
oblonga, 626
Cylindrosporium Pomi, 463
Cyme, **338,** 339
Cyperaceae, 800
Cyperus, Brown, **801**
fuscus, **801**
Cyphomandra betacea, 745
Cypress, 301
Cypripedieae, 911
Cypripedium, 925
Cystidia, 505
Cytase, 138
Cytisus Adami, 989
Cajan, 633
Laburnum, 989
purpureus, 989
Cystopteris bulbifera, 331
Cystopus candidus, 520
Cytoplasm, **15,** 18
Cytoplasmic inheritance, 974

Dactylis glomerata, 799
Dactyloides, 835
Daemonorops, 856
Daffodil, **280,** 895
Hoop-Petticoat, 895
Dahlias, 970
Dairy, bacteria and the, 544
Daisy, White, 791
Yellow, 791
Dalbergia, 633
Damping-off fungus, 520

Dandelion, **333**, 381, 791
Darwin, 947, 949, 983, 995, **1007**
Darwinism, present status of, 1010
Darwin's theory, 1007
Dasheens, 876
Date merchants, **865**
Date palms under cultivation, number of, 865
Date-palm, 863, **864**
Date Plum, 724
Dates, transportation of, 866
Datura, 966
Daucus Carota, 709
Daughter-nucleus, 23
Day-flower, 879
De Bary, Heinrich Anton, 487
Decay, 145, 199
Decline, internal, 654
Deductive reasoning, 922
Deficiency, 979
Dehisce, 9
Dehiscent, 407
Deliquescent, 426
Delphinium, 596, 946
Dematium, 212
Demerec, 974
Dendrobium crumenaium, 803
nobile, **918**
Dendrocalameae, 804
Dendrocalamus giganteus, 802
strictus, 803
Dentrification, 232
Denitrobacterium denitrificans, 232
Desert vegetation, types of, **100, 122**
Deserts, 89
Detlefsen, 994
Deutzias, 612
Devil's Paint Brush, 791
Dewberries, 615
Diadelphous, 7
Dianthus, 591
barbatus, 591
Caryophyllus, 591
Diapensaceae, 719
Diapensia Family, 719,
Diapensia lapponica, **720**
Diastase, animal, 138
Diatoms, 447
Dicentra spectabilis, 606
Dicksonia punctilobula, **281**
Dicotyledonous, 71
Dicotyledonous plant, morphology of a typical, **352**
Dicotyledons, 354
monocotyledonous, **355**, 356
Dicotyledony, 354
Dictamnus, 645
Didynamous, 739, 774
Diervilla, 782
Diffusion, 45
Digitalis, 775
Digitaria, 798
Dihybrid, 976
Dimorphy, **378**
Dioecious, 341
Dioecious habit, 373
Dionaea muscipula, **193**
Dioscorea alata, 733, 893
Batatas, **894**
bonariensis, **355**, 794
bulbifera, 893
divaricata, 894
villosa, 895
Dioscoreaceae, 893
Dioscorides, 639
Diospyros, 721, **724**
Dendo, 725
Ebenum, 725
melanoxylon, 725
Montana, 725
quaesita, 725
reticulata, 725
tomentosa, 725
Diphylleia cymosa, 602
Diploid, 24, 417
Dipsacaceae, 782
Dipsacus fullonum, 782
Dischidia rafflesiana, 100, **102**
Disease carriers, 537
Disease, combating, 538, 541
contagious and infectious, 537
Diseases, resistance to various, 999
Dissimilation, 196
Distribution, geographical, 569

Division, heterotypic or differential, 972
second reducing, 974
Docks, 584
Dodder, **216,** 217, 218, 732
Dodecatheon, 720
Dodoens, 833
Dogbane Family, 726
Dogberry, 613
Dog's-tooth violet, **347,** 885, 887
Dogwood, 965
Dogwood Family, 705
Dogwood, Flowering, **335,** 337
Dolichos, 632
biflorus, 633
lignosus, 632
Dominance, law of, 958
Dominant, 953
Dropper, 324
Drosera, 973
intermedia, **195**
rotundifolia, **328,** 331
Drosophila, 973, 978, 979, 980, 994
melanogaster, 961
Drought, definition of, 81
enduring, 95
escaping, 94
evading, 110
frequency, 93
periods of, 89
protection against, 94
seasonal, 89
sporadic, 92
weeds and, 84
Drug, 560
Drupaceae, 627
Drupe, 407, 860
Dry farming, 126
Dryobalanops aromatica, 604
Duchesne, Antoine Nicolas, 372
Duckweeds, 877
Ducts, 75
Duplication, 979
Durra, 826
Dust mulch, 128
Dutchman's Breeches, 606
Dwarf Varieties, 126
Ear of corn, what is an, 846
Early blight of Potatoes, 463, 769
Earth-stars, 479
East, E. M., 984, 994
Ebenaceae, 723
Ebenales, 720
Ebony, 725
Ebony Family, 720, 723
Echeveria gibbiflora metallica, **100**
Echinocactus emosyi, **96**
Echinocereus, 98
Echinochloa, 797
crus-galli, 823
frumentosa, 823
Edibility, Criterion of, 517
Eel-grass, **320, 361,** 362, 796
Egg, 345
Egg-cell, 413
Egg-plant, **770,** 771, 944
Elaeagnus, **238**
Elaeis guineensis, **152,** 855, 862
Elder, 782
Electric light, growing plants in, 177
Elements, essential, 159
Elephant ear, 876
Elephants, breeding of, 1008
Eletteria Cardamomum, 909
Elm Family, 576
Elodea, **14,** 16, 52, 380, 797
canadensis, 380
iowensis, 380
Embryo, 9, 11, **417, 429,** 435
Dicotyledonous, **352**
Monocotyledonous, **353**
Embryogeny, perpetual, 302
Embryo-sac, 345, **346,** 819, 851
Emmer, 814, 966
Endemis vacciniana, 719
Endive, 790
Endocarp, 407, 627, 858, 860
Endo-enzymes, 140
Endogenous, 70
Endosmosis, 52
Endosperm, 189, 354, 435
horny, **852**
nucleus, primary, **345,** 849

Endosperm of corn grain, 583
soft, **859**
starchy, **852**
Endospores, 136
Endothia parasitica, **523, 524**
Enteromorpha compressa, 238
Envelope, Floral, 347
Environment, 271, 944
fitness for, 1008
heredity, variation and, 935
variation due to, 943
Enzymes, 131, 143
action of, 138
kinds of, 137
Epiblast, **355,** 812
Epicarp, 858
Epidendreae, 911
Epidermis, 57, 72
Epigaea repens, **715**
Epigynous, 350
Epinasty, 256, 288
Epipactis, 916
pubescens, 926
Epiphyllum, 921
Epiphyte, **100,** 204, 208
Epiphytism, 208
Epipogon aphyllus, 921
Epithelium, 812, **852**
Equisetum arvense, **552**
palustre, **552**
Eranthis, 336
Ergot, **521**
Erica carnea, 712
melanthera, 712
vagans, 712
Ericaceae, 711
Ericales, 711
Eriocaulaceae, 878
Ervum Lens, 628
Erythronium, **347,** 885, 887
Etiolation, 282
Eubambuseae, 804
Eubasidiomycetes, 479
Eucalyptol, 699
Eucalyptus, 694
globulus, 695, **696, 699**
punctata, 698
Eucalyptus rostrata, 699
Euchlaena mexicana, 834, 835
Eugenia aromatica, 692, **693**
caryophyllata, 692
Eugenol, 694
Eu-mycetes, 463
Euonymous atropurpureus, 657
japonicus, 988
Eupatorium perfoliatum, 791
purpureum, 791
Euphorbia, **97, 98**
Esula, 321
Euphorbiaceae, 638
Evaporation in United States, Chart showing, **127**
Evening-Primrose Family, 689
Evening-Primrose, Lamarck's, **690**
Evergreens, Broad-leaved, 334
Evetria buoliana, 543
Evolution, 564, 1001, 1004
and religion, 1012
floral, 410
of structures, 570
organic, 1009
regressive, 878
theories of, 1006
Evolution vs. transformation, 1005
Excurrent, 426
Existence, struggle for, 1008
Exocarp, 627
Exosmosis, 52
Experimental method, 942
Experiments, Mendel's, 949
Exudation, 76
Eyes, 759

Factors, 958, 960
complementary, 988
generalization on, 985
Fagales, 587
Fagogyrum, **346**
esculentum, **584**
Fagus, 587
Fallow, Value of, 447
Falls (of Iris), 899
False Indigo, **344**
False Solomon's Seal, 891, 892

Families, 560
Fanwort, 592
Farinha, 644
Faris, 1000
Farming, dry, 126
Fasciation, 962
Fascicle, **338,** 339
Fats, 159, 185
Fawn Lily, 887
Femaleness and maleness, 548
Fermentation, 155
alcoholic, 132, 141
biological significance of alcoholic, 141
to our daily lives, relation of, 142
Fermentation-tube, **132,** 133
Fermentations in agriculture, 142
Fern, Bladder, 331
Boston, 968
fertilization in the, **416**
Hay-scented, 281
life history of a, 410
Walking, 331
Ferns, 970
Filmy, 546
Fertility, 166, 951
Fertilization, 352, 852
double, **346,** 352
in the fern, **416**
Fibro-vascular bundle, closed, **71**
Ficus, 577
aurea, 578
benghalensis, **578**
Carica, 578
elastica, **74,** 577, 643
populnea, 578
pumila, 577
religiosa, 577
repens, 577
Fig, Creeping, 577
Figs, Breba, 581
Capri, **579,** 580, 581
Edible, 578
Florida Strangling, 578
Goat, 580
Higo, 581
Profichi Capri, **579,** 580
Figs, Smyrna, 580
Wild, 580
Figwort, **375,** 775
Figwort Family, 774
Filament, 7
Fire blight, 536
Fish-grass, 592
Fishes, disease of, 220
Fittest, origin of the, 1011
survival of the, 1009
Flax, 357
Common, **635, 636,** 945
New Zealand, 887, 886
Flax Family, 634
Floral envelopes, 7
Florets, 6
Flour, entire wheat, 812
graham, 813
patent process, 812
Flower, anatomy of an angiospermous, **343**
complete, 340
Hermaphrodite, 340
perfect, 340
pistillate, 340
staminate, 340
Flower-color forms, 965
Flowering, gregarious, 803
Flowering Maple, 183
Flowers, 207
meaning of, 335
Monoecious, **341, 342**
Fly agaric, **504**
Focke, 992
Foliage leaf, structure of a, 55
Follicle, 407
Fomes applanatus, **532**
Food organic, all, 199
storage of, 188
translocation of, 185
Foods, kinds of, 159
Foot (in Ferns), **417,** 442
Forests, conservation of, 121
Formation (Plant), 205
Forms, physiological, 486
Forsythia, 731
Fortuitous, 968

Fortunella japonica, 651
Fothergilla, 614
Four-o'clock, 968, 970
Foxgloves, 775
Foxtail grass, 797
Fragaria, **319**
chiloensis, 615, 617
elatior, 616
vesca, 617
virginiana, 615
Fraxinus, 726
Fritillaria, 391
imperalis, 887
meleagris, 887
Frog-spittle, 455
Frog's bit, 797
Fronds, 410
Fruit, 8
aggregate, **359**
fleshy, 407
formation of, 358
simple, 406
Fruit spot of apples, 463
Fruit worm, 719
Fruits, accessory, 408
aggregate, 408
classification of, 406, 409
multiple, 408
parthenocarpic, 770
Fuchs, Leonhard, 562, 689
Fuchsia, 391, 689
Fucus, **450**, 451
Fuligo septica, **514**
Fumaria officinalis, 606
Fungi, edible, 517
number of species of, 463
origin and classification of, 462
smut, 487
timber-destroying, 532
true, 463
Fungi-imperfecti, 463
Fungus, endtrophic, **921**
rust, 480
what is a, 460
Fungus-farms, 205
Fungus-gardens, 205
Funiculus, 9, 11, 344
Fusarium oxysporum, 769
Fusion-nucleus, 345, 849

Gailardia, 791
Gaines, 987, 1000
Galanthus nivalis, 190
Galapagos islands, 392
Galax, 719
Galium, 776
Galton, Francis, 937, 947, 995
Galtonia, **289**
Gama grass, 798, 835
Gametangia, 469, 476
Gametes, 414, 962
Gametic, 962
Gametophyte, 414
Garber, R. J., 947, 960
Garcinia mangostana, 689
Garden Heliotrope, 782
Gardenia, 782
Gardner, 992
Garland Flower, 910
Garlic, **324**, 882
Gas plant, 645
Gases, exchange of, **148**, 151
Gasteria, **289**
nigricans, **100**
Gasteromycetes, 479
Gaylussacia, 716
Geitonogamy, 366
Gelidia, 447
Gels, 18
Gemmae, 305, 545
Generalizations, Mendelian, 975
Generation, F_1 or first filial, 952, 953
Generation, second hybrid (F_2), 952, 953
Generations, alteration of, 418
Generative-cell, 433
Genes, 958, 960
and chromosomes, 975
arrangement of the, 980
stability of, 967
Genetic terms, 960
Genetics or practical breeding, applied, 997
Genotypes, 960

Genotypic, 960, 962
Gentianales, 726
Gentian Family, 726
Genus, 560
Geophilous habit, 105
Geotropism, 272, 274
  negative, **276**
  positive, **275**
Geranium, **286, 287,** 943
  Strawberry, **611**
Geranium Family, 634
Gerard, John, **749**
Gerardias, 775
Germ tube, **473**
Germ-cells, 962
Germination, 10, 351
  cavity, 682
  delayed, 153
Gherkins, 784
Gideon, 1000
Ginger, 745, 908
Ginger ale, 745
Ginger Family, 909
Ginger-Lily, **909**
Ginseng, 705, **706,** 707
Ginseng Family, 705
Gladiolus, 946, 992
Gland, racemose, **192**
Gleditsia triacanthos, 628
Gleocapsa gigas, 459
Gleosporium nervisequum, 267
Globeflower, **333,** 336, 347, 595
Glomerule, **338,** 339
Glory-Flower, **374**
Glume, 337, **818,** 837
  flowering, 799
Glycine Soja, 628, 820
Glycogen, 460
Glycyrrhiza, 628
  glabra, 628
Gnetum, 566
Golden Club, 875
Golden-bell, 731
Golden-rods, 791
Goldthread, 595
Gooseberries, 612, **613,** 1000
Gooseberry Family, 612
Gooseberry, Wild prickly, **613**
Goosefoot Family, 587
Gosio, vital reaction of, 551
Gossypium, 665, 671
Gourd, 407, 783
Gourd Family, 783
Graft-hybrids, 988, **990**
Grafting, 241, 310, **312**
Grain standards, 807
Grama grass, **34**
Gramineae, 798
  subdiivsions of, 801
Grape, 315
  Concord, 661
  Edible stemmed, 98
  European, **659**
  Merrimack, 395
  Northern Fox, **661**
  Seedless, 662
  Southern Fox, **662**
Grape Family, 658
Grapefruit, **652,** 653, 946, 963
  Marsh Seedless, 947
Grape-Hyacinth, 887
Grapes in Mesopotamia, irrigation of, 121
Grass Family, 798
Grass, Gama, 835
  Grama, **34**
  Johnson, **824**
  Sudan, **825**
Grass-embryos, **355**
Grass-of-Parnassus, 612
Gravity, relation of roots and stems to, 272
Gray, Asa, 572
Green Brier, **892**
Green Silk, 455
Grossularia, 612
Grossulariaciae, 612
Groups, systematic, 559
Growth and nourishment, 253
  and osmosis, 245
  differential, 247
  effect of light on, 267
  experiment in, 246

Growth in thickness of stems, secondary, 259
permanent and temporary, 252
Guard cells, 58
Guards (in peony), **601**
Guava, Common, **692**
Strawberry, **691**
Guayule, 643
Gulden-Appelen, **744**
Gum, chewing, 723
Gumbo, 668
Guncotton, 669
Gunnera, 218
manicata, 218
Gutta Percha, 721, **722**
Guttation, 76
Gymnocladus dioica, 628
Gymnosperm, 429
Gynoecium, 343, 350
Gynophore, 631
Gypsophila, 591

Habernaria lacera, **332**
Haematoxylon campechianum, 633
Haemoderaceae, 895
Haemophila, 979
Hagerdoorn, 997
Hales, Stephen, 723
Halesia carolina, 723
Halophytes, 170
Hamamelidaceae, 613
Hamamelis arborea, 614
Japonica, 614
mollis, 614
vernalis, 614
virginiana, 614
Zuccariniana, 614
Hand, 1000
Hansen, 1000
Haplophyllum, 644
Haploid, 24, 417
Harebell, 788
Haw, 619
Hawkweed, 791
Hawthorn, 619
Hay-Fever, and Pollen, 401
Hayes, 947, 960, **984,** 994
Hazel-nut, 587
Head, **337,** 339
Heal-all, 740
Heart's-ease, 680
Heath, Cornish, 712
Heath Family, 711
Heather, **712**
Hedera helix, 66
Hedge Mustard, 608
Helianthemum, 679
Helianthus, **73**
Helianthus, 791
tuberosus, 791
Heliothis armiger, 675
Heliotropism, 272
Hellebore, 595
Helleborus, 596
Helmont, Johannes Baptiste van, 173
Hemerocallis, 883
Hemibasidiomycetes, 479, 489
Hemi-basidium, 489
Hemiparasites, 218
Hemp, **381, 581, 582**
African Bowstring, **886,** 888
Manila, 906, **907**
Sisal, 897, **898**
Henequen, 897, **898**
Hepatica, 336, 348
Hercules Club, **56,** 707
Heredity, 936
physical basis of, 971
Heredity, variation and environment, 935
Herpetomonas, 218
Hesperidium, 407
Heteranthera, 879
Heterodera radicicola, 675
Heteroecism, 480
Heterogamy, 549
Heterosis, 983
Heterospory, 422, 550
Heterostyly, 375
Heterothallic, 470
Heterotypic division, **23**
Heterozygosis, 983
Heterozygote, 961

Heterozygous, 961
Heuchera, 611
Hevea brasiliensis, 639, **640, 641**
guyanensis, 640, 649
Hibisceae, 668
Hibiscus, 668
esculentus, 665, 668
Hicoria, 587
Hieracium aurantiacum, 791
Hilum, 9, 11
Hippeastrum, 895
Histology, 57
Hogs, mule-footed, 963
Hohenbergias, 99
Holcus halepensis, **798**
Sorghum sudanensis, 830
Holdfast, **455**
Holly, 334
American, 657
English, 657
Holly Family, 657
Hollyhocks, 946
Homology, 436
Homospory, 422, 549
Homothallic, 470
Homotypic, 974
Homotypic division, **23**
Homozygotes, 961
Homozygous, 961
Honey Locust, 628
Honeysuckle, Japanese, **781**
Swamp, 714
Wild, 714
Hooke, Robert, 15
Hop, 256, 583, 584, 1000
Hop-tree, 645
Hopi Maize, 115, **118**
Hordeae, 806, 816
Hordeum, **799, 817**
distichum, 816
Vulgare, 816
Hormone, 282
Hornbeam, **176, 177,** 587
Horsechestnut, 658
Horse-radish, 608
Houseleek, **319,** 334, **943**
Spiderweb, 609
Huckleberries, 716
Hulls, 821
Humulus lupulus, 256, **583,** 584
Humidity, soil, **82, 83**
Humming birds, 391, 930
Humus, 146, 201
Huxley's Simile, 140
Hybrid, 961
Hybridization, 947, 961
Hybridizing, 366
Hybrids, 958
Walnut, 985
Hydathodes, 59, 60, **61, 62**
Hydnaceae, 479
Hydrangea, 945
Hydrangeaceae, 612
Hydrolysis, 140
Hydrotropism, 272, 285, **287**
Hygiene, personal, 538
public, 538
Hymenium, 503, **504**
Hymenocallis occidentalis, 895
Hymenomycetes, 479
sexuality in the, 509
Hymenophyllaceae, 546
Hymenophyllum, 545
Hypericaceae, 679, 689
Hypericum perforatum, **344**
prolificum, 344
Hyphae, 460
Ascogenous, 476
Hypocotyl, 10, 11, 353
Hypogynous, 350
Hyponasty, 255, 288
Hypothesis, 136, 1003
Multiple, 1003
Working, 1003
Hypoxis, 895
Hypsophylls, **333,** 336, 349

Iberis, 608
Ibervillea sonorae, **94**
Ilex, 334
Aquifolium, 657
crenata, 657
glabra, 657
opaca, 657

Ilex verticillata, 657
Imbibition, 51
Immunity, 537
Impatiens, 381
Inbreeding, 961
Inbreeding, effects of prolonged, 371
Indehiscent, 407
Independent Assortment, Law of, 959
Indian corn, **60**, 69, **115, 192, 254,** 384, **385**
Indian pipe, 200
Indian Root, 707
Indian Tobacco, 789
Indian-pipe Family, 719
Indicator for crops, natural vegetation as an, 124
Indigo, 628
Indigofera tinctoria, 628
Inductive method, 922
Inflorescence, 6, 335, 338, 339
Influences, historical, 24
Ingen-Housz, Jan, **172**
Ingrafting, 539
Inheritance, 1008
Injections, plant, 164
Inkberry, 657
Ink-cap fungi, 549
Innovation (branches), **442**
Inoculation, 539
Inoculation, legume, 243
of non-legumes, 243
of soils, 241
Inorganic, 167
Insectivorous plants, 194
Insects, flowers and, 207
Insertion, 105
Integument, 345, **429**
Interference, 975, 981
Internodes, 105
Intertillage, 123
Invertase, 137
Involucre, **333**
Ions, 45
Ipomoea Batatas, 732, **733, 735, 736, 738**
Ipomoea leptophylla, 34
Iridaceae, 898
Iris, **899**, 946
pseudacorus, 898
versicolor, 898
Iris Family, 898
Ironwood, 587
Irrigation, **90**, 119
Irritability, 21, 271
Isospory, 549
Itea virginica, 612
Ivory, Vegetable, 855
Ivy, English, 66, 707
Poison, 657

Jack-in-the-Pulpit, 337, **872, 875**
Jambosa Caryophyllus, 692
Jeffersonia diphylla, 602
Jerusalem Artichoke, 791
Johannsen, 942, 996
Nineteen Beans of, 994
Johnson-grass, **798**
Johny-jump-up, 680
Jones, D. F., 984
Jones, L. R., 1000
Juglandales, 587
Juglans cinerea, 587
nigra, 587
regia, 587
Juncaceae, 800
Juncus, **381**
effusus, **801**
June drop, 395
Juneberry, 619
Jussieu, Antoine Laurent de, 559
Jute, 665

Kafir, 826
Kaki, 724
Kale, **607**
Kalmia, 388
angustifolia, 714
latifolia, **389, 714, 715**
Kaoliang, 826
Kataphyll, 336, 337
Keel, 7
Kelp Groves, 453

Kelps as fertilizer, 452
Kelps, Giant, 448, **449**
Kentucky Coffee-tree, 628, **778**
Key, 407
Kieffer, 1000
Klebs, 943
Kleinia, **98**
ficoides, **100**
Knight, Thomas Andrew, 274, 754
Knight's experiment, 273
Knots, 426
Knotweed, Japanese, **318**
Knotweeds, 584
Koelreuter, Joseph Gottlieb, **364**
Kohlrabi, **607**, 608
Kumquat, 651

Labellum, **910**, 916
Labiatae, 738
Lace Leaf, **379, 380**
Lachnanthes, 895
Lactuca sativa, 790
scariola, 790, **940**
Laelia, 927
Lamarck's Hypothesis, 1006
Lambkill, 714
Lamella, middle, 626
Larkspur, 596
Late blight, 521, 769
Lathyrus, 991
odoratus, 628
Lauraceae, 602
Laurel, 388
Cherry, 66, 334
Sheep, 714
Laurel Family, 602
Laurus canariensis, 604
Layering, **307**, 317
Leadwort Family, 720
Leaf, 4
tissues of a, 57
Leaf, free-living, 878
Leaf, Lace, **380**
Leaf-base, 6
Leaf-blade, 4
Leaf-fall, 102, 104
Leaf-miner, 219
Leaf-mosaic, 291, **293, 294**
Leaf-parenchyma, 57
Leaf-scar, 103
Leaf-sheath, **799**
Leaf-stalk, 4
Leaflet, 4
Leaves, growth of, 250
significance of, 174
Lecanora esculenta, 213
Leek, Wild, 882
Leersia clandestina, **355**
Leeuwenhoek, Anton van, 134
Legislation concerning blister rust of pines, 532
chestnut disease, 523
cotton, 670
currants and gooseberries (planting), 532
grapes, 660
importing plants, 543
pines, planting of, 532
pollination, 401
spraying, 401
weeds, 84
wheat rust, 524
Legume, 237, 406, 407
Legume inoculation, 243
Leguminous crops, necessity of, 240
Leitneriales, 587
Lemma, 799, **818**, 877
trisulca, **875**
Lemnaceae, 878
Lemoine, 1000
Lemon, 649, 653, 654
Lemons, brown rot of, 520
internal decline of, 654
Lenticels, **151**, 628
Leonurus Cardiaca, **297**
Lepidium sativum, 608
Leptochloa arabica, **355**
Lessonia, 451
Lethals, 987
Lettuce, 790, 939, **941**
Lettuce, Wild, **940**
Leucothoe, 334
Liana, 803
Lichen, **208, 209, 210**

Lichen produced synthetically, **211**
Lichens, economic importance of, 213
Licorice root, 628
Liebig, 135
Life-cycle, 12
Light, effect of, on direction of growth, 277
electric, and growth, 177
on rate of growth, 282
relation of leaves to, 284
Ligulate, 614
Ligule, 798, 799, 836
Ligustrum Ibota, **730**
ovalifolium, **729,** 730
vulgare, 730
Lilac, 727, 728
Liliaceae, 881, 887
Liliales, 880
Lilies, 946
day, 883
Lilium bulbiferum, 883
canadense, **324, 346**
candidum, 883
elegans, 883
Harrisii, 883
Japonicum, 883
longiflorum, 883
Martagon, **351, 883**
philadelphicum, **883,** 884
superbum, 884
tigrinum, **324,** 883
Lily, American Turk's Cap, 884
Easter, 883
European Turk's Cap, 883
Madonna, 883
Swamp, 895
Tiger, 883
Wood, **883**
Lily Family, 881, 887
Lily-of-the-Valley, 892, 970
Lily-of-the-Valley Sub-family, 889
Lime, 654
Limiting factor, 161
Limnobium, 797
Limonium, 720
Linaceae, 634
Linaria vulgaris, **773, 774**
Linden, **70, 258, 260, 265, 665**
Linden Family, 665
Lingua, 88
Linin, 20
Linkage, 975, 977, 979
negative, 977
partial, 977
sex, 979
Linkage groups, 975, 979
limitation of the, 979
Linnaea, 782
Linnaeus, **562,** 563, 666
Linseed, 634
Linum
angustifolium, 635
grandiflorum, 357
grandiflorum rubrum, 636
perenne, 635, 636
ustitatissimum, **635,** 636
Lipase, 137
Liquidamabar, 614
Liquidambar Styraciflua, 614
Liquorice root, 628
Liriodendron tulipifera, **175,** 593
Little-Club-Moss, 420
Little Potatoes, **519,** 769
Liverwort, **306**
life history of a, 444
Livistona australis, 152
Lizard's tail, **59, 573**
Lobelia, 788
cardinalis, 789
inflata, 789
Locus, 980
Locust, 628
Lodicules, **818**
Logania Family, 726
Logwood, 633
Loment, 407
Lonicera, 782
Japonica, **781**
Loosestrifes, 720
Lophiola, 895
Lotus, 593
East Indian, 153
Love Apples, 743

Lucerne, 111, 629
Lungs of plants, 147
Lunularia, **306**
Lupine, White, **74**
Lupines, 633
Lupinus affinis, 390
albus, **74,** 272, **283**
arboreus, 633
Lychnis, 591
dioica, 979
Lycoperdon giganteum, **513**
Lycopersicum, **313,** 394
cerasiforme, 745
esculentum, 742, **744**
pimpinellifolium, 745
pyriforme, 745
Lygodesmia juncea, 34
Lysimachia, 720

Mace, **356,** 357
MacGillivray, 974
Maclura, 577
Macrocystis, 451
pyrifera, 454
Madder Family, 776
Magnolia, 375
Magnolia Family, 593
Magnolia, Flower of, **592, 593**
Magueyes, 896
Maheleb, 627
Mahogany Family, 655
Maianthemum, 892,
Maidenhair Fern, **417**
Maiosis, **23**
Maize, 383, 961, 966, 968, 992
Hopi, 115, **118**
Navajo, 115, **117**
Pollen produced by, 848
Zuni, **116, 120**
Marjoram, Sweet, 741
Mala punica, 700
Malapoenna, 602
Maleness and femaleness, 548
Mallow, Indian, 665, 668
Marsh, 668
Musk, 665, 668
Rose, 668
Mallow Family, 668
Mallows, 665
Malt, 816
Maltase, 137
Malus baccata, 619
floribunda, 619
pumila, 619
sylvestris, 619
Malva, 668
moschata, 665
Malvaceae, 665, 668
Malvales, 665
Malveae, 668
Mamme, 581
Mandrake, 602
Mangifera indica, 656, 657
Mango, 657, **656**
Mangosteen, 689
Mangrove, 109, 701, 702
Black, **701**
Red, 702
Mangrove Family, 701
Mangrove swamp, **704**
Manihot, 643
aipi, 644
utilissima, 644
Manna, 213
Bamboo, 805, 806
Manometer, 77
Maple Family, 657
Maple, sugar, 657
Maple-scale, Cottony, 211
Maranta, 902
Marantaceae, 911
Marchant, Nicholas, 444
Marchantia polymorpha, 444, **445, 446**
Marggraf, 995
Marguerite, 791
Mariposa Lily, 887
Marsh Rosemary, 720
Marshmallow, 665
Mary, Typhoid, 537
Mathiola, 608
Mathonia, 602
Mavor, 968
Maxillaria, 927

Mayapple, 602
Mayflower, 715, 892
Meadow Mushroom, 501, 505
outline of life history of, 511
Meadow-grass, 385
Medeola, 892
Medicago falcata, **327**
sativa, 111, 629
Medulla, 71
Medullary rays, secondary, 262
Megasporangia, 421, **422,** 429
Megaspore, germinating, 423
Megaspores, 421, **429,** 550
Megasporophylls, 421
Megasporophytes, 551
Meliaceae, 655
Melipona, 930
Melocanneae, 804
Melons, Honeydew, 784
Membrane, limiting, 19
nuclear, **15,** 19
plasma, 19
Mendel, **948,** 949, 954, 959
Mendel, hypothesis, 965
Mendel's experiments, 949
Mendel's laws, 958
Mentha, 740
anarvensis, 740
arvensis, 740
piperita, 740
spicata, 740
Mercerising, 675
Mescal, 879
Mesocarp, 407, 859
Mesocotyl, **852**
Mesophyll, 62, 57
Metabolism, 20, 197
Metachlamydeae, 571
Metaphase, 23
Method, experimental, 942
inductive, 922
scientific, 1002
statistical, 940
Metroxylon, 856
Micheli, Pietro Antonio, 217
Micro-organisms in the soil, 244
Micropyle, 9, 11, 345, **429**
Microsphaera Alni, **472, 473**
life history of, 474
Microsporangia, 421, **422**
Microspore, germination of, 431
Microspores, 421, 431, 550
Microsporophylls, 421
Microsporophytes, 551
Midgets, 963
Mignonette, 606
Mildew, Downy, 521, 769
Lilac, **472, 473**
Powdery, 472, **473**
Millet, Barnyard, 823
Broom-corn, **822,** 823
Foxtail, 823
Hog, 823
Proso, 823
Milo, 826
Milkweed, 356, 389, **390,** 726
Milkweed Family, 726
Milkwort Family, 655
Mimosa Family, 627
Mimosa pudica, **252**
Mimosaceae, 627
Mimosoideae, 627
Mimusops globosa, 723
Mineola vaccinii, 719
Mineral elements, source of the, 160
Mint Family, 738
Mirabilis, 993
Mire-grass, **125**
Mistletoe, **219**
Mitchella repens, 776, **777**
Mitella, 611
Miterwort, False, 611
Mitochondria, 20
Mixed population, 942
Mohl, Hugo von, 15
Mold, Blue, 474
Mold, life-cycle of a dioecious, **470,** 471
Molds, 533
Molds and bacteria, nitrogen-fixation by, 237
Monkshood, 392, 596
Monocotyledon, dicotyledonous, **355,** 356

Monocotyledonous, 70
Monocotyledonous plant, morphology of typical, **353**
Monocotyledons, 354
Monoecious, 340
Monoecious habit, 374
Mono-hybrid, 976
Monopodial, 917
Monotropa Hypopitys, **201**
uniflora, 200
Monotropaceae, 719
Monstera deliciosa, **336, 874,** 877
Montagu, Lady Mary Wortley, 540
Moraceae, 576
Morchella esculenta, **478**
Morel, **478**
Morgan, 968, 975, 981
Morning glory, 992
Morning-glory, Bush, **125**
Morning-glory Family, 731
Morphine, 605
Morus alba, **939**
rubra, **577**
Moss, **306**
Florida, **878,** 879
Flowering, 719
Hair-cap, 438, **439**
Moss-rose, 1008
Mosses, 438
Black, 440
Peat, 441
Moth, Yucca, **888**
Mother of thousands, **611**
Mother-cell, **22**
Motherwort, **297**
Mountain Ash, 619
Mountain Laurel, **389, 714, 715**
Moutan, 598
Movements, Carpotropic, 358
Mucor, 468
mucedo, 533
stolonifer, 533
Mud-plantain, 879
Mulberry, Paper, 577
Red, **577**
variation in, **939**
White, 577
Mulberry Family, 576
Mulch, dust, 128
Mullein, **112, 276,** 775, 880
Muller, H. J., 967
Multiplication, vegetative, 466, 546
Musa Cavendishii, 906
ensete, 906
glauca, 906
Nepalensis, 906
paradisiaca, 906
rubra, 906
sapientum, **55, 903, 904, 905**
textilis, 906, 907
Musaceae, 902
Muscadine, 661, **662**
Muscari, 887
Mushroom, Common, **512**
Horse, **506**
Meadow, **512**
Shaggy-mane, **518**
Mushroom culture, 518
Mushrooms and Toadstools, 517
Muskmelons, 784
Mustard, Black, **606**
Chinese, 608
White, 609
Mustard Family, 606
Mutability, rate of, 968
Mutant, 963
Mutation, **964,** 1011
gene, 968
types of, 963
variation due to, 962
Mutation theory, 1012
Mutations, 968
animal, 963
classes of, 966
generalizations concerning, 967
germinal or seed, 963
somatic, vegetative, or bud, 963
Mutilations, agricultural, 197
Mutualism, 208
Mycelium, 460
Mycorhizas, 646
ectotrophic, **214**
endotrophic, **214**

Myrica, 586
cerifera, 586
Myricaceae, 586
Myricales, 586
Myristica fragrans, 595
Myristicaceae, 594
Myrmecophytes, 205
Myroxylon Pereirae, 628
toluiferum, 628
Myrsiphyllum, 891
Myrtaceae, 690
Myrtales, 689
Myrtle Family, 690
Myrtle, wax, 586
Myxomycetes, 514, **515**

Nabours, 978
Nägeli, Carl Wilhelm von, 136
Naiadales, 796
Names, scientific, 557
Narcissus, **280,** 895, 966
poeticus, **896**
Narcissus-fly, 219
Nasturtium, **285,** 293, 400
Naudin, 947
Navajo Maize, 115, **117**
Neck, 413
Neck-canal, 413
Nectandra, 602
Nectarine, 962
Nectary, **348**
Nelumbo lutea, 593
nucifera, 153, 593
Nemalion, 448
Andersonii, **449**
multifidum, **449**
Neottia Nidus-avis, 920, **921,** 923
Neottieae, 911, 916
Nepenthes, 99
ampullaria, 383
Nepeta Cataria, **740**
Nephrolepis cordifolia, **322**
tuberosa, **322**
Nereocystis, 451
leutkeana, 448, 454
Nerium oleander, **114**
Nest-fungi, 479
Nettle, stinging, 584
Nicaragua, 387
Nicotiana, 80, 994
rustica, 772
tabacum, 771, **772,** 972
Nightshade, **771**
Nile, 88
Nilsson-Ehle, 987
Nitragin, 243
Nitrates, formation of, 228
Nitric acid, formation of, 228
Nitrification, 227
Nitrites, formation of, 227
Nitrobacter, **227**
Nitrobacterine, 243
Nitrogen, direct utilization of free, by green plants, 231
circulation of in nature, **240**
importance, of, 222
loss of, 222
need of, 222
sources of, 225
Nitrogen-cycle, 240
Nitrogen-fixation, 233
by molds and bacteria, 237
Nitrosomonas, **227**
Nitrous acid, formation of, 227
Node, 105
Nodules, non-leguminous, 238
Nomenclature, 557
Non-cross-overs, 977
Non-legumes, inoculation of, 243
Norton, J. B., 1000
Nostoc, 211
pruniforme, **459**
Nourishment and growth, 253
Nucellus, **429**
Nuclear division, **22**
Nuclear sap, 20
Nuclear skein, **22**
Nuclei, 347
polar, 849, **851**
Nucleolus, **15,** 20
Nucleoplasm, **15,** 19
Nucleus, 16, 19
endosperm, **346**
generative, 346, **347**

Nucleus, primary endosperm, 345, **346,** 849
tube, 346, **347**
Nuphar, 592
Nut, 407
Nutation, **255**
Nutmeg, **356,** 595
Nutmeg Family, 594
Nutrients, mineral, 161
Nutrition, agricultural, 197
Nymphaea, 593
Daubeniana, **331**
micrantha, **331**
Nymphaeaceae, 592

Oak, 63
live, 334
poison, 657
Oaks, 587
Oases, 90
Oats, 66, 391, 805, 817, **818, 853,** 987, 1000
Oats, life-cycle of loose smut of, **495**
loose smut of, 493
Wild, 66
Ocimum Basilicum, 741
Ocotillo, 66
Odontoglossum, 925
Oenothera, 979, 987
gigas, 966
Lamarackiana, 689, **690**
Officinalis, meaning of, 560
Offsets, 324
Ohga, Ichiro, 153
Oidium lactis, 477
Oil, Bergamot, 650
linseed, 634
Oil-palm, **152,** 855, 862
Okra, 665, 668
Olea, **726**
europaea, 726
Oleaceae, 726
Oleander, 114
Olive, **726**
Olive Family, 726
Olive-knot, 727
Onagraceae, 689
Onion, **324,** 882
umbel of, **881, 882**
Wild, 882
Onions, "Multiplier," 323, 882
reserve food in, 190
top, 882
Onoclea Struthiopteris, **246**
Oögonia, **449,** 451, **452, 454**
Oolong, 685, 686
Oömycetes, 462
Oösperm, 417
Oöspora scabies, 769
Oöspore, 417
Operculum, 442
Ophrydeae, 911
Opium, 605
Opuntia Blakeana, **220**
camanchica, **96, 97**
Orange, **644,** 645, 939, 946, 999
bitter, 650
Mandarin, 650
Navel, 963
Osage, 577
Satsuma, 651
Seville, 650
sweet, 650
varieties of, 649
Orchard crops, remedy for failure of, 396
successful, 394
Orchard grass, 799
Orchid, **207,** 332, **388,** 911, **912, 913**
Orchid, air-root of an, **919**
Bird's-nest, 920, **921**
Pigeon, 803
seedling of an, 925
Orchid flower, Darwin's description of an, 912
ground plan of an, **912**
Orchid seed, 921
germination of, 921, **923, 924**
non-symbiotic germination of, 927
Orchidales, 911
Orchids grow in colonies, why certain, 926
grown on agar, 925

Orchids, quantity of seeds produced by, 927
roots of, 919
symbiosis in, 920
sympodial, 918
Orders, 560
Organ, 14
Organic, 167
Organic cycle, **158**
Organism, 14
Origanum Majorana, 741
Origin of species, 949
Ornithogalum, 887
Orobanchaceae, **215**
Orontium, 875
Orpine Family, 611
Orris root, 900
Orthotropous, **345**
Orton, 999
Oryza sativa, **820**
Oryzeae, 820
Oscilatoria violacea, **459**
Osmosis, **48**
Osmosis and growth, 245
Ostrich Fern, **246**
Ostrya, 587
Ovary, 8, 342
inferior, 350
superior, 350
Ovulary, 343
Ovule, orthotropous, **346**
Ovules, 343
Oxalidaceae, 655
Oxalis, **286**
Acetosella, 391
bupleurifolia, **253**
Oyster Plant, 790

Pachycereus, **98**
Paddy rice, 231, 821
Paeonia albiflora, 596, **599**
Moutan, 598
officinalis, 600
suffruticosa, 598
Paeony, 381
Palaquium Gutta, 721, **722**
Palea, 838
Palets, 337
Palisade layer, 63
Palisade parenchyma, 63
Palm, Barrigona, **276, 855**
Cabbage, 856
Coconut, **857, 858, 859**
Royal, **855**
Talipot, 803
Palmales, 855
Palmetto, 859
Palus, 871
Panax quinquefolium, 705, **706**, 707
Pandanales, 796
Panic grass, 799
Paniceae, 823
Panicle, **337**, 339, **818**
Panicum, 799
Panicum latifolium, 798
miliaceum, 822, 823
Pansy, 680
English, **681**
Papaver Rhoeas, **794**
setigerum, 605
somniferum, 605
Papaveraceae, 605
Papaw, North American, 594
Papaya, **687, 688**
Papaya Family, 686
Papayaceae, 686
Papilionaceae, 627, 628
Papilionoideae, 627
Pappus, 357
Paraphyses, 504
Parasites, artificial, 220
facultative, 221
Fungal, 220
obligate, 221
Parasitism, 216
Parenchyma, 70
palisade, 63, **76**
spongy, 64, **76**
Parietales, 678
Parmelia perlata, **209**
Parmentier, Antoine-Augustin, 750
Parnassia, 612
Parnell, 974
Paronychia jamesii, **35**

Parsley, 708
Parsley Family, 705, 708
Parsnip, 709, 710
Parthenium argentatum, 643
Parthenocarpic fruits, 770
Parthenocarpy, 745
Parthenocissus, 664
Parthenogenesis, 550
Partial linkage, 977
Partridge-berry, 776, **777**
Passifloraceae, 679
Passion Flowers, 679
Pasteur, Louis, 135, 535
Pasteurized, 306
Pastinaca sativa, 709, **710**
Pathogenes, 541
Paulownia, 775
Payena, 721
Pea, **254, 255,** 406
  Australian, 632
  Family, 627, 628
  Garden, 628
  Pigeon, 633
  Sweet, 628
  two types of flowering branches, 953
Peach, 962
Peach leaf-curl, 521
Peaches, 963
Peanut, **359, 360, 630**
Peanut field, **631**
Pear, **395,** 619, 630, 939, 1000
  Bartlett, 395, **623**
  Flanish Beauty, 395,
  Kieffer, 395, 396
  Sickel, 395
Pearl, Raymond, 979
Peas, 968, 969, 972, 988
  Chenille, **967**
  differentiating characters in, 951
  experimental results involving a single pair, 952, 954
  varieties of, 950
Pectin, 18, 44
Pedicel, 6, 335
Peduncle, 6, 335
Peepul tree, 577
Pelandra, 875
Pelargonium, **286, 287,** 634, 975
Peliss, **809**
Pellionia Daveauana, **181**
Penicillium, 474
  camemberti, 477
  glaucum, 476
  roqueforti, 477
Pentad, **809**
Pentstemon, 775
Peonies, 946
Peony Flower, 598
  Herbaceous, **596, 597, 600**
  Tree, **596,** 597
Peperomia Saundersii, **575**
Pepo, 407
Pepper, Black, **574**
Pepper, Cayenne, 745
Pepper-grass, 608
Peppermint, 740
Peppers, Red, 745
Pepsin, 138
Perennials, 190, 333
Perianth, 347
Pericarp, 406
Periderm, 263
Peridermium pyriforme, 529
  Strobi, 529
Perigynous, 350
Perisperm, 189, 354, 435
Perithecium, **473,** 474
Persea, 602
Persea carolinensis, 603
Persimmon, 721, **724**
  Japanese, 724
Peruvian bark, 777
Petalody of carpels, 347
  of stamens, 347, **348, 618**
Petaloids, **600, 601**
Petals, coalescence of, **348**
Petiole, 4
Petiolule, 4
Petroselinum graveolens, 708
  hortense, 708
Peziza sylvestris, **478**
Phalaenopsis, 926

Phaseolus, **254, 255**
multiflorus, 392
vulgaris, **387,** 628
Phellandrene, 699
Phelloderm, 262
Phellogen, 262
Phenotypic, 962
Philadelphus, 612, 727
Philotria, 797
Phleum pratense, 799, **819**
Phloem, 71, 72
secondary, 262
Phlox, 732
Phoenix dactylifera, 863, **864, 867, 869**
farinifera, 856
Phormium tenax, 887
Phosphates, 230
Photoperiodism, 269, 723
Photosynthate, 182
Photosynthesis, 178, **179,** 183
Photosynthesis and leaf symmetry, correlation between, 182
Phototropism, 272, 278
Phragmidium violaceum, **484**
Phragmites, 966
Phycocyanin, **459**
Phycomycetes, 462
Phycomycetes, diseases caused by, 520
Phyllophore, 870
Phylloxera vestatrix, 315, 660
Physalis pubescens, 745
Physcia stellaris, **208**
Physiology, 14
Phytelephas macrocarpa, 855
Phytolaccaceae, 588, 590
Phytophthora infestans, 521, 769
Phytoptus, **520**
Pickerel-weed, **378,** 877
Pickerel-weed Family, 879
Pie-plant, 584
Pigweeds, 590
Pilea pumila, 584
Pimenta officinalis, 694, **695**
Pimpernel, 720
Pine, **427**
Pine, Austrian, **431**
leaf of a, **114**
life history of the, 426
life-cycle of a, **435**
pollen grains of, **382**
White, **432, 433**
Pineapple Family, 879
Pineapples, **879, 880,** 946
Pine-drops, 719
Pine-shoot moth, 543
Pinguicula, 794
Pinguicula caudata, **355**
vulgaris, **355**
Pink Family, 588, 591
Pinus austriaca, **431**
Strobus, **432, 433**
sylvestris, **428, 429**
Pinxter, 714
Piper Betle, 574
Cubeba, **574**
magnifica, **572**
nigrum, **574**
Piperaceae, 573
Piperales, 571
Pipewort Family, 878
Pipsissewa, 719
Pistil, 8, 341, **381**
Pistils, compound, **344**
Pisum, **254,** 935
sativum, 406, 628, 961
Pitcher Plant, **356,** 338
Pith, 71, 72
Pixie, 719
Placenta, 9, 344, 568
Placentation, 344, 568
Plane Tree Family, 615
Plant association, 205
Plant diseases and bacteria, 535
Plant diseases, fungi that cause, 518
Plant foods, chemical composition of, 159
Plant nutrition an electrical phenomenon, 165
Plant propagation, 303
Plant quarantines, 543
Plant secretions, economic value of, 197

Plantago, 375, 880
Plantain, 375, 880, 906
Platanus, **267**
Plant-hairs, 6
Plants, Dioecious, 552
Plants, double-flowered, 962
Plasmodiophora brassicae, **515**
Plasmodium, 514
Plasmolysis, 52
Plastid, 15, 16
Pleurococcus, 457, 546
life history of, 305
vulgaris, **303, 458**
Plowing, reasons for, 128
Plum, 398
Plum Family, 627
Plum pockets, 521
Plumbaginaceae, 720
Plumule, 10, 353, **852**
Pneumathodes, **152**
Poa compressa, 385
pratensis, 799
Poaceae, 798
Poateae, 801
Podetia, **210**
Podophyllum peltatum, 602
Poinsettia, 337
Pokeweed Family, 588, 590
Polemoniales, 731
Pollen, 7, 346
and hay-fever, 401
chamber, **429**
distance carried, 383
immediate effect of, 357
quantity of, 381
storage and shipment of, 399
viability of, 384, 386
Pollen-grains, 346
Pollen-tube, 433
Pollination and horticultural practice, cross, 393
and legislation, 401
and plant evolution, insect, 392
and plant geography, insect, 392
other agents of, 390
Pollinium, 389, **916**
Pollinosis, 403
Polyadelphous, 668
Polycarpaea spirostylis, 164
Polycotyledony, 354
Polyembryony, 647
Polygala polygama, 391
Polygalaceae, 655
Polygamous, 380
Polygonales, 584
Polygonatum, 892
Polygonatum biflorum, **106**
Polygonum, 584
Sieboldii, **318**
Polypetalae, 571
Polyporaceae, 479
Polyporus betulinus, **513**
Polyrrhiza funalis, 918
Polystichum, **412**
acrostichoides, **411**
adiantiforme, **412**
Polytrichum commune, 438, **439**
Pomaceae, 618
Pome, 407
Pomeae, 618
Pomegranate, **700**
Pomegranate Family, 699, **700**
Pomelo, 653
Poncirus trifoliata, 649
Pondweeds, 796
Pontederia cordata, 378, **877**, 879
Pontederiaceae, 879
Popcorn, 854
Poplar, 585
Poppy Family, 605
Poppy, opium, 605
Populus, 585
Pores, germination, **860**
Portulaca, 591
Portulacaceae, 588, 591
Potamogeton, 796
Potato, 60, **321, 746, 748, 753,** 762, 790, 1000
air, 893
Burbank, 751
Chinese, **894**
diseases, 769
Family, 742
flowering and fruiting of, 769

Potato fruit, **747**
leaf, 768
root system, **39, 40**
rot, 521
seed germinating, **752**
seedling, **753**
Sweet, 732, **733, 735, 736, 738**
Potato tuber, **188, 765, 767**
developed in light, 758
effect of size of seed-piece on sprouting, 766
Potato tubers, sweetening of, 144
Potatoes, 946, 947
early blight of, 463
Potato-tree, 746
Prescottia plantaginea, 921
Pressure, exudation, 77
negative, 78
Prickly Ash, 645
Priestley, Joseph, **174**
Primary endosperm nucleus, 345
Primordia, 347
Primrose, Chinese, 936
Primrose Family, 720
Primrose order, 719
Primula, 966, 968, 979
Primula japonica, **721**
sinensis rubra, 936
Primulaceae, 720
Primulales, 719
Prince's pine, 719
Pringle, 1000
Privet, **729**
California, 730
European, 730
Ibota, 730
Processing, 725
Production, excessive, 1008
Pro-embryo, 435
Profichi, Figs., 581
Proliferating, **210**
Proliferation, 438
Promycelium, 479, 483, 489
Pronuba yuccasella, **888**
Propagation, artificial, 307
leaf, 309
natural, 317
Prophylaxis, 403
Protease, 137
Proteins, 159
manufacture of, 185
Proterandrous, 739
Proterandry, **374**
Proterogyny, **375,** 848
Prothallus, 412, **413, 414, 415, 418**
Protobasidiomycetes, 479, 480
Protocorm, 926
Protonema, 412, **413,** 440
Protoplasm, 15
chemistry of, 21
Protoplast, 16
Protoxylem, 71
Prune, 396, 398
Prunella, 740
Pruning, 123
bad, 104
natural, 426
Prunus Amygdalus, 627
avium, 992
domestica, 398
laurocerasus, 66, 334
Mahaleb, 627
maritima, 627
Padus, **326**
pennsylvanica, 627
virginiana, 627
Psedera, 664
Pseudomonas radicicola, 211, 235
Psidium cattleianum, 691
Guajava, 691, **692**
Psoralea, **125**
tenuiflora, **86,** 125
Ptelea, 644, 645
Pteridium aquilinum, **413**
Pterocarya, 587
Ptomaine, 145
Ptyalin, 138
Puccinia graminis, 480, **481, 482, 485**
podophylli, **484**
Puff-balls, 479
Pulque, 897
Pulvinaria, 212
Pulvinus, 253, 671

Pumpkins, 784
Punic apples, 700
Punica Granatum, **700**
Punicaceae, 699
Punnett, 977, 980
Punnett square, 956
Pure cultures, 243
Pure lines, 996
Purslane Family, 588, 591
Putrefaction, 145
Pycnidium, 485
Pycnium, 485, 486
Pycnospores, 486
Pyrenoids, 457, 549
Pyrolaceae, 719
Pyrus, **395,** 619
  baccata, 619
  communis, 621
  Malus, 619
  serotina, 621
Pythium de Baryanum, 520
Pyxidanthera, 719

Quarantine, 538
Quarantines, plant, 543
Quercus, 587
  rubra, **261**
  suber, 263
  Virginiana, 334
Quick grass, 798
Quince, 626
Quince, Flowering, 626
Quinidine, 781
Quinine, 777, 781

Raceme, **337,** 339
Races, physiological, 542
Rachis, 811, 868
Radicle, 295, 852
Radicula Armoracia, 608
Radicula Nasturtium-aquaticum, 608
Radish, 608
Ragweed, **791**
Rainfall, distribution of annual, **126**
Ranales, 592
Ranunculaceae, 595
Ranunculus, 347, **348**
Ranunculus aquatilis, 379
Rape, 609
Rapeoil, 606
Raphanus Raphanistrum, 608
  sativus, 608
Raphe, 356
Raphia Ruffia, 856
Raphides, 877
Raspberries, 615
  American red, **616**
  New Zealand, **57**
Rattan, 856
Rattle-snake-plantain, 926
Ray, John, **354,** 563
Rays, medullary, 71
  pith, 71
Reaction, 21
Reasoning, deductive, 922
Receptacle, 6
Recessive, 953
Red Clover, 5, 11
Red Fife, **808**
Red Gum, 699
Red Oak, **261**
Red rust stage, 480
Reduction, 972
Reduction division, **23**
Redwoods, 301
Reed, 1000
Reforestation, 237
Regeneration, **311**
Reimer, 1000
Reindeer moss, 213
Religion and evolution, 1012
Renanthera, 918
Reproduction by spores, 546
  cell-division and, 545
  essence of, 302
  types of, 302
Repulsion, 977
Resedaceae, 606
Respiration, **148,** 150, 155, 183
  plant and animal, 153
Rest period, 143, 760
  cause of the, 759
Resting nucleus, 23
Resurrection Plant, 124

Retting, 637
Rhabdopterus picipes, 719
Rhamnaceae, 658
Rhamnales, 658
Rheum rhaponticum, 584
Rhinanthoideae, 774
Rhine River, 88
Rhizoctonia, **519,** 925
Rhizoctonia, 925
Rhizoid, **413,** 446
Rhizome, 105, 410
Rhizomorphs, 501
Rhizophora Mangle, 109, **701, 702**
Rhizophoraceae, 701
Rhizopus, 461
nigricans, **462,** 463, **464, 465, 466, 467,** 533
sexuality of, 470
Rhododendron, 381, 712, 713
Rhopobota vacciniana, 719
Rhubarb, 584
Rhus quercifolia, 657
Toxicodendron, 657
typhina, 656
vernix, 656
Ribes, 612
americana, 613
Cynosbati, **613**
Grossularia, 613
hirtellum, 613
nigrum, 613
rubrum, 612, **613**
vulgare, 357, 613
Rice, **820**
Rice, fields, fighting weeds in, 85
Paddy, 231, 821
rough, 821
Rices, Wild, 822
Richardia, 875
Richwood, 584
Ricinus, **254,** 992
communis, **72, 638, 639, 938**
Rigor mortis, 18
Ring, cotyledonary, 354
Ripening, 626
Rippling, 637
Robinia Pseudoacacia, 109, 628
Robins, albino, 963
Rock Roses, 679
Rogues, 946
Root competition for moisture, 86, 166
Root, free-living, 921
Root system, **37, 38, 39, 40**
extent of, 33
in action, 170
Root-hairs, 40, **42, 43**
Root-louse, 315, 660
Root-nodules, **212,** 234
Root-pressure, 76
Roots, aerial, **918**
branches of, 267
buttressing, 265
contractile, **107,** 710
distribution of, 86
elongation of, 249
formation of fibrous, **308**
of orchids, 919
tuberous, 330
Rootstock, 105
Root-tip in tropisms, function of the, 279
Root-tubercles, **11,** 234, **238**
Rosa, **618,** 966
arkansana, 34
Rosaceae, 615
Rosales, 610
Rose, 347, **618**
Rose Family, 615
Rose hip, 408
Roses, 992
Rosette, 769
Rostellum, 913, 930
Rotation, 16
Rotmistrov, 81
Roystonea oleracea, 856
regia, **855**
Rubber, Assam, 643
Ceara, 643
Central American, **642**
Commercial, 639
Rubber Tree, Para, **640, 641**
Rubber-plant, **74,** 577
Rubiaceae, 776

Rubiales, 776
Rubus, **359**
Australis, **57**
strigosus, **616**
Rudbeckia hirta, 791
Rue, 644, 645
Rue Family, 644
Rue-Anemone, **348**
Rumex, 584
Runners, **319**
Rush, **381**, 801
Rushes, 800
Rusts, 524
Ruta, 645
graveolens, 644
Rutabaga, 608
Rutaceae, 644
Rye, 66, 805, 815

Sabal palmetto, 859
Sac Fungi, 472
Saccharomyces, 135, **136**
Saccharum officinarum, 831, **833**
Saddle grafting, **990**
Saffron, 901
Sage, 740
Scarlet, 740
Sagittaria, **342**, 796
Sago, 855
Salicaceae, 585
Salicin, 586
Salix, **308**
discolor, **585, 586**
Salmon, 1000
Salsify, 790
Salvia, 739
azurea grandiflora, 740
officinalis, 740
sclarea, 741
splendens, 740
Salvinia, 218
Samara, 407
Sambucus, 782
Sand Spurrey, 591
Sandwort, 591
Sanguinaria canadensis, 605
Sanitation, 538
Sanseviera guineensis, 886
Sap, 68
ascent of, 76, 80
Sapindaceae, 658
Sapindales, 655
Sapium, 643
sebiferum, 185
Sapodilla, 723
Sapodilla Family, 721
Saponaria, 591
Sapotaceae, 721
Saprogenic, 145
Saprolegnia, 220
Saprophile, 145
Saprophytes, 200
Saprophytism, 199, 200
Sarcocarp, 858
Sarracenia, 99
purpurea, **356**
Sarsaparilla, 705
Wild, 707
Sassafras, 602
Nepal, 605
officinale, 604
tzumu, 604
variifolium, 603
Satureia hortensis, 741
Saururaceae, 571
Saururus cernuus, **59, 573**
Saussure, Nicolas Theodore de, 172
Savory, Summer, 741
Saxifraga sarmentosa, **611**
Saxifragaceae, 611
Saxifrage, **344**
Golden, 612
Saxifrage Family, 611
Scab, 769
Scale, ovuliferous, **429**
Scheuchzeriaceae, 796
Scientific method, 173
Scitaminales, 902
Sclerenchyma, 72
Sclerotinia ledi, 480
Scotch pine, **428, 429**
Screw-pine, 796
Scrophularia, 375, 775
nodosa, **375**

Scrophulariaceae, 774
Scutching, 637
Scutellum, **355, 813,** 852
Sea Lavender, 720
Sea-kale, 588
Seaweeds, Brown, **449**
Secale cereale, 805, 815
montanum, 816
Secretion of water in leaves, 78
Sedges, 800
Sedum spectabile, 611
Sedum Treleasei, **100**
Seed, disease-free, 946
formation of the, 434
how made, 351
selfed, 961
Seed-coat, maturing of the, 356
Seed-habit, 108
Seeds, appendages of, **356**
Seef-heal, 740
Segregation, 958
law of, 958
Selaginella, 420, 423
amoena, **421**
Martensii, 422
Selection, 994
clonal or bud, 999
line, 998
mass, 998
natural, 1009
Self-colored, 885
Selfed, 961
Self-heal, 740
Selfing, 369
Self-pollination, 366, 368, 391
Self-pruning, 103, **104**
Sempervivum, **943**, 334
arachnoideum, **609,** 611
tectorum, **319**
Senebier, Jean, 172
Senna, Wild, 628
Sensitive plant, **252,** 628
Sequoia gigantea, 301, 333
Serrate, 6
Serum-therapy, 540
Serviceberry, 619
Seta, 439
Setaria, 797
italica, 823
Sets, 882
Sex, chemical differences of, 551
determination of, 551
meaning of, 554
transformation of, by smut infection, 498
Sexes, structural differentiation of the, 550
Sex-organs, differentiation of, 550
Sexuality in the Hymenomycetes, 509
Shad bush, 619
Shaddock, 653
Shaggy-mane mushroom, **518**
Shallots, 882
Sheath, 798
Shelf-fungi, 220, **532**
Shin-leaf, 719
Shooting Star, 720
Shoots, long, 621, **622**
Shull, 984
Sieve-tubes, 71, 72, 75
Silene, 591
odontipetala, **794**
Silicle, 606
Silique, 606
Silk, 844
Silver Bell, 723
Silverberry, **238**
Simarubaceae, 655
Sinker, 324
Siphonales, 455
Sisal Hemp, **898**
false, 898
Sisymbrium, 608
Sisyrinchium, 898
Skunk Cabbage, 107, 375, 875
Slime-mold, **514**
Sloan, Hans, 110
Smilacaceæ, 892
Smilacina, 891
Smilax Family, 892
Smilax herbacea, 892, **893**
rotundifolia, **892**
Smilax of florists, 890, 893

Smilax, tendrils of, 259
Smut, crop losses from, 499
infection, modes of, 497
infection, transformation of sex by, 498
of Barley, covered, **496**
of Oats, loose, 493, 495
of Wheat, life-cycle of Loose, **490**
of Wheat, stinking, **491, 492**
Smuts, 524
comparison of cereal, 500
Snails, 391
Snapdragon, 774, 979
Snowberry, 782
Snowdrop, 190
Soapberry Family, 658
Soapwort, 591
Soil, 224
Soil, cultivation of the, 128
Soil ingredients, uses of, 170
Soil moisture, conservation of, 88
distribution of, 81
Soil-bacteria, 230
Soils, inoculation of, 241
Solanum, **313**
Dulcamara, **771**
maglia, 750
melongena, **770,** 771
nigrum, **771,** 972, 991
tuberosum, **311, 746, 747, 748,** 759
Tubingense, **990**
verbascifolium, 746
Solidago, 791
Solomon's seal, **106,** 892
Sols, 17
Solute, 45
Solvent, 46
Sorbus, 619
Sorghum, grain, 826
kafir, **827**
milo, **828**
Sorghum Halepense, **824**
Sorghums, 1000
hay, 826
Sorgo, 826
Sorgo, Gooseneck, **828**
Sorosis, 879
Sorus, 411, **412, 413**
Sour-sop, 594
Soybean, 628
Spadix, **336,** 337, 339, **873**
Sparganiaceae, 796
Spartina cynosuroides, **355**
Spathe, **336,** 337, 872
Spearmint, 740
Species, 559
Speed-wells, 775
Spelt, 833, 966
Spergularia, 591
Sperm, **851**
Spermagonium, 486
Spermatia, 486
Spermatophyte, 425
Sperm-cells, 434
Sperms, 414, **416**
Sphaerotheca phythoptophyla, **520**
Sphagnales, 441
Sphagnum acutifolium, **441**
cuspidatum, **442**
economic importance of, 443
Spicebush, 604
Spiderwort, **876**
Spiderwort Family, 879
Spike, **337,** 339
Spikelet, 798, **818**
Spikenard, American, 707
Spinach, 590
Spinacia oleracea, 590
Spiraea, 615
Spirem, 22
Spirogyra, 19, 304, 455, **456, 548**
longata, **457**
Splice grafting, **990**
Sporangia, 411, 412
Sporangiophore, 467
Sporangium, **464, 465, 466, 467**
Spordium, 483
Spore formation, 461
Spore-fruit, 474
Spore-mother-cell, 24
Spores, development of basidium and, **510**

Spores, discharge of, 505
in high altitudes, 508
motile, 461
number of, 507
promycelial, 494
reproduction by, 546
sexual differentiation of, 549
Sporogonium, 439, **446**
Sporophore, 483
Sporophylls, 411, **412**
Sports, bud, 963, **965,** 970
seed, 963
Spurge, 321
Spurge Family, 638
Spurs, 621
apple, **621**
Spur-shoots, **622**
Squares, 672
Squash, **784**
Crookneck, 783
seed, germination of, 786, 787
Turban, 784, **785**
Staff-tree Family, 657
Stamens, 7, 345
petalody of, 347, **348, 618**
Staminodes (Staminodia), **600,** 601, **618,** 910
Standard, 7
Standards, 899
Standards, grain, 807
Stapelia variegata, **98**
Star grass, 895
Starch grains, **181, 188, 190, 191**
Starch-formers, 549
Starch-making, 180
Star-of-Bethlehem, 887
Steironema, 720
Stem structure, dicotyledonous, 70
monocotyledonous, 69
Stem-cutting of *Diervilla*, **310**
Stem-rot, 769
Stem-rust, Black, **523**
of wheat, 480
of wheat, loss from, 480
Stems, elongation of, 249
Sterculia, 667
Sterculia Family, 666
Sterculiaceae, 666
Sterigma, **476,** 461, 503
Sterility, 993
Sticktights, 791
Stigma, 8, 341
Stimulus, 21, 271
Stinging Nettle, 584
Stipe, **360,** 501, 631
Stipules, 6
St. Johnswort, Common, **344**
St. John's-wort Family, 679, 689
Stocks, 608
Stolons, 318, **319**
propagation by, 731
Stoma, 58
Stomata, 59, **60,** 151
number of, 58
sunken, 113
Stooling of cereals, 944
Storax Family, 721, 723
Strawberry, **319,** 408, 615, 617, 946, 970
Strawberry War, 372
Streaming, 465
Streptopus, 892
Strophiole, **352,** 357
Struggle for existence, 1008
Style-canal, **351,** 844
Styracaceae, 721, 723
Styrax Benzoin, 614, 723
Suberin, 103
Sub-hymenium, **505**
Subsoiling, 128
Substratum, 463
Succory, 789
Suckers, 266, 318
Sugar beets, 945
Sugar cane, **308,** 831, **833,** 946
planting, **832**
Sugar, Maple, 658
Sugar-apple, **594**
Sulphur-bacteria, 184
Sumach, Poison, 656
Staghorn, 656
Summer Hyacinth, **289**
Sundew, **195,** 331
Sunflower, **73,** 791

Sunflower, red, 965
Sunlight, importance of, 177
Surface, limiting, 19
Surgery, antiseptic, 540
Survival of the fittest, 1009
Suspensor, 434
Sutton, 971
Suture, 9
Swamp, 711
Swamp Cypress, knees of 152
Sweet Pea, 961, 977, 991, 980
Sweet Pepperbush, 719
Sweet Potatoes, 946
Sweet William, 591, 732
Sweet-Alyssum, 608
Sweetfern, 586
Sweet-Flag, 875
Sweet-gale Family, 586
Sweet-leaf Family, 721
Sweet-sop, **594**
Swietenia Mahogani, 655
Swingle, 1000
Sycamore, **267**
Symbiosis, **202**
evolution of, 921
Symbiosis in Orchids, 920
Symbols, 960
Sympetalae, 571
Symphoricarpos, 782
Symplocaceae, 721
Symplocarpus, 375
Symplocarpus foetidus, 875
Sympodial, 917
Synapsis, **23**
Synconium, 339, 408, 578
Synergids, 849, **851**
Syngenesious, 789
Synizesis, **23**
Synura, 448
Syringa, 727
japonica, 728
persica var. *laciniata*, 728
pinnatifolia, 728
sempervirens, 727
vulgaris, 728
Syrup, maple, 658
Systematic botany, 557
Systematic relationships and genetics, 996

Tabasco sauce, 745
Tail-flower, 337, 875
Tallow-tree, 185
Tamus communus, **355,** 794
Tanacetum vulgare, 791
Tangelo, 651
Tangerines, 650
Tansy, 791
Tape-grass Family, 796
Tapioca, 644
Tap-root, 8
Taraxacum, **333,** 381, 791
Taro, 876
Taxodium distichum, 152
mucronatum, 301
Taxonomy, 557
Tea, 683, 679, **684**
Black, 685
Green, 685, 686
Teasel, Fuller's, 782
Teasel Family, 782
Tecoma, 775
radicans, **356,** 357
Tectoria cicutaria, **330,** 331
Teleutospores, 483
Telispores, 483, **484**
Teosinte, **834,** 835
Ternstroemiaceae, 679
Testa, 357
Testudo sumeirei, 301
Tetrad-division, 24
Tetradynamous, 606
Tetraphis, **306**
Thalia, 902
Thea sinensis, 679, **684**
Theaceae, 679
Thein, 686
Thelephoraceae, 479
Theobroma cacao, **666, 667**
Theophrastus, 561, 639, 868
Theory, 136, 1003
Thigmotropism, 272
Thistle, 791
Thorn-apple, 619

Thoroughwort, 791
Thrips, 390
Thyme, 741
Thymus, vulgaris, 741
Thyrsus, 339
Thysanoptera, 390
Tiarella, 611
Tiger Lily, **324**
Tilden, 1000
Tilia, **70**, 665, **258, 260, 265**
americana, 665
heterophylla, **665**
michauxii, **665**
Tiliaceae, 665
Tillandsia, **204**
usneoides, **878**, 879
Tillering, **317**
Tilletia laevis, **491**, **492**
tritici, **494**
Timothy, 799
inflorescence of, **819**
Tip worm, 719
Tischler, 966
Tissue, 14
Tissue-tension, 247, **248**
Toad-flax, **773, 774**
Toadstool, 501
Toadstools and Mushrooms, 517
Tobacco, **381**, 391, 771, **772**, 962, 968, 980, 983
fasciated variety of, **964**
Toluifera Balsamum, 628
Tomato, 385, 394, 742, **744**, 944, **990**, 991
Cherry, 745
Currant, 745
Musk, 745
Pear, 745
Tree, 745
Tomato-fruit worm, 675
Top-soil, 146
Tortoise, Aldabra, 301
Torus, 358
Toxin, 145
Toxylon, 577
Tracheids, 75
Tradescantia, **344**, 879
Tradescantia virginiana, **876**
Tragopogon porrifolius, 790
Tragus, 562
racemosus, 800
Trailing Arbutus, **715**
Trama, 505
Transfer of foods, is there a lateral, 186
Transformation, evolution *vs.*, **1005**
Transpiration, 64
advantage of, 67
control of, 65
current, 68
effect of spraying on, 66
lifting power of, 78, **79**
reduction of, 111
Trapa natans, 355, 794
Traumatropism, 272
Trees, Weeping, 276
Trefoil, Shrubby, 645
Tremellineae, 479
Trichogyne, **449**
Trifolium hybridum, 358
pratense, 4, **5**, 109
Trillium, 892
Trioecious, 380
Triple-fusion, 352
Tripsaceae, 832, 835
Tripsacum, 835
dactyloides, 798
Triticum, 807, 966
aestivum, 807
dicoccum dicoccoides, 814
durum, 810
hybernum, 807
sativum campactum, 811
sativum turgidum, 811
sativum vulgare, 810
turgidum, 811
vulgare, **355, 805**, 810
Trollius, 336, 347, 595
Europaeus, **333**
laxus, **333**, **349**
Tropaeolum, 58
majus, **285, 293**, 400
Tropisms, 271

Tropisms in agriculture, importance of, 292
Trumpetcreeper, 356, 357
Trumpetcreeper Family, 775
Trypsin, 138
Tschermak, Erich von, **948**
Tube, stylar, **347**, 351
Tube-algae, 455
Tube-cell, 432
Tuber, Potato, **755, 756, 757, 758**
structure of a, 754
Tubercles, Leguminous, 234
Tubers, Aerial, 757
formation of, **321**
for seed, preparation of, 764
in a fern, **322**
with ingrowing sprouts, Potato, 757
within tubers, 756
Tulip, 884
Tulip Droppers, 885
Tulip, reproduction of, 325
Tulipa Gesneriana, 884
suaveolens, 884
sylvestris, 106
Turcarum, 884
Tulip-mania, 884
Tulips, breeder,
Tuliptree, **175**, 593
Tumors, **536**
Tundras, 89
Turgor, 51
Turnip, 608
Turtleheads, 775
Twin-flower, 782
Twining plants, 258
Twinleaf, 602
Twisted-stalk, 892
Typha angustifolia, **795, 796**
latifolia, 795, 796
Typhaceae, 796
Typhoid fever, 537
Typhoid Mary, 537

Ulmaceae, 576
Ulmus americana, **576**
Ulothrix, 548
Ulothrix zonata, **547**
Umbel, **337**, 339
of Onion, **881**
Umbelliferae, 705, 992
Umbrella Leaf, 602
Unit characters, 960
Uredinales, 479, 480
Uredinia, 480
Urediniospores, 480, **484**
Uredo, 480
Uredo stage, 480
Uredospore, 480
Urtica dioica, 584
Urticaceae, 584
Urticales, 575
Ustilaginales, 479, 487
Ustilago avenae, 493
hordei, **496**
kuhneana, **494**
maydis, **499**
nuda, 496
scabiosae, **494**
segetum, **494**
tritici, **488**
violacea, 487
zeae, 498
Utricle, primordial, 18
Utricularia grafiana, **194**
neglecta, **194**

Vacciniaceae, 716
Vaccinium, 716
corymbosum, **368**, 369, **716**, 717
erthrocarpum, 717
macrocarpon, 717
Oxycoccus, 717
Vacinnation, 539
Vacuoles, 18
contractile, 19, **457**
Valerian Family, 782
Valerianaceae, 782
Vallisneria spiralis, **320, 361,** 362, 796
Vallisneriaceae, 796
van Fleet, 1000
Vanda, 966
Vanilla, artificial, 931

Vanilla, Balsam of, 931
Vanilla, 918, 927, **928**
hand pollination of, **930**
planifolia, **928, 929**
Variation, 937, 1008
and environment, heredity, 935
due to crossing, 947
due to environment, 943
fluctuating, 1011
in Mulberry, **939**
in seeds of Castor Oil Bean, **938**
methods of studying, 940
rate of, 940
Varieties, double-flowered, 963
pure-breeding, 958
resistant, 542
running out of, 945
Vaucheria, **455,** 549
sessilis, **454**
terrestris, 454
Veins, 6
Velamen, **919,** 920
Venter, 413
Venus's flytrap, **193**
Verbascum, 880
Thapsus, **112, 276,** 775
Verbena ciliata, 66
Verbenas, 946
Veronica, 775
Versatile, 384
Verticilaster, 339
Vespucci, Amerigo, 815
Viburnum Opulus, 719
Viburnums, 782
Vicia Faba, 632
chromosome cycles in, **973**
Victoria Cruziana, **591,** 593
regia, 593
regia Trickeri, 593
Vigna catjang, 632
sinensis, 632
Vilmorin, P.L.F.L., 590, 976, 995
Vine, Balloon, 658
Vinegar, 544, 626
Vinegar fly, 961, 966
Vino di banana, 907
Viola altaica, 680, **681, 682**
Viola blanda, **679,** 680
cornuta, 679
cucullata, 680
cornuta, 679
lutea, 680
odorata, 679, 680
palmata, 680
tricolor, 680
Violet Family, 679
Violet, Sweet White, **679**
Virginia Creeper, 664
Virginia Willow, 612
Virgin's Bower, 595
Vitaceae, 658
Vital reaction of Gosio, 551
Vitis capensis, **103**
Labrusca, 315, **661**
quadrangularis, 98, 99
rotundifolia, 661, **662**
vinifera, 315, **659,** 663
Vries, Hugo de, **948,** 1011

Waahoo, 657
Wake Robin, 892
Walking Fern, 329
Wallace, 995
Wall-cell, 433
Wallflower, 386, 608
Walnut, 983
Black, 587
Circassian, 587
English, 587
Walnuts, antagonism of the, 587
Wardian cases, 642
Waring, 1000
Water Arum, **873,** 875
Water Bamboo, 823
Water, capillary, 44, 129
combined, 108
duty of, 32
gravitational, 129
hygroscopic, 108, 129
in crop plants, percentage of, 30
requirements of plants, 30, 31
storage of, 95
Water Chestnut, 794
Water table, 83

Waterlily Family, 592
Waterlily, White, **356,** 592
Yellow, 592
Waterplantain, **797**
Waterplantain Family, 796
Watercress, 608
Watermelon, 784, 999
Water-pore, 59
Water-shield, 593
Waterweed, 380, 797
Weather, 124
Weathering, 166
Webber, 1000
Wedge grafting, **990**
Weeds, legislation against, 84
Weeping Trees, 276, 944
Weigela, 782
Weinstein, 981
Wheat, 66, **381,** 391, **805, 806,** 966, **997,** 999, 1000
bunt of, 494
embryo, 813
germination of, 153
grain, **853**
harvesting and threshing, **814**
loose smut of, **488**
loss from stem-rust of, 480
Marquis, 807, **808**
primary roots of, **36**
rust, **481, 482, 485**
section of a grain of, **812**
spring, 807
stinking smut of, **491, 492**
straw, 800
types of, 806
winter, 807
Wheats, Durum, 809
Hard Red Spring, **808**
White Lupine, **283**
White Mustard, **278, 279**
White weed, 791
White-alder Family, 719
Whitewood, 593, 594
Whorls, 350, 426
Wild Elder, 707
Wild Hyacinth, 887
Wild Lettuce, 112, **113**
Wild Prickly Gooseberry, **613**
Wild Radish, 608
Willow Family, 585
Willow, Glaucus, **585, 586**
Willows, weeping character of, 962
Wilt, 769
Wind, 224
Windflowers, 595
Wing, 357
Wings, 7
Winkler, 990
Winogradsky, 227
Wintergreen Family, 719
Wistaria 628
Witches' Broom, **520,** 521
Witch-hazel, 614
Witch-hazel Family, 614
Wolffia, 877
papulifera, **875**
punctata, **875**
Wood, annual layers of, **261**
secondary, 262
Wood-sorrel, Family, 655
Woodwardia orientalis, 331, 546

Xanthosoma, 876
Xanthoxylum, 644, 645
X-chromosome, **553**
Xenia, 853
Xenogamy, 366
Xeno-parasitism, **220**
Xerophytic, 802
Xylem, primary, 72
Xyridaceae, 878
Xyridales, 878

Yam, 734, 894
Chinese, 894
greater, 893
Yam Family, 893
Yam-root, 895
Yautia, 876
Yeast, 131, 136
what is, 134
Yellow Adder's Tongue, 887
Yellow Flag, 898
Yellow Poplar, 594

Yellow-eyed-Grass Family, 878
Yucca, 334
filamentosa, **887, 888**
Yukon River, 88

Zea canina, 835
Zea Mays, **115, 192**, 231, 254, **355, 357**, 384, 385, 832, **833, 835, 838, 839, 840, 841, 842, 843, 844, 847, 849, 850, 851, 852**
leaf of, **839**
Zea Mays, indentata, **37**
Zeleny, 968
Zelkowa, 576
Zingiber officinale, **908**, 909
Zingiberaceae, 909
Zizania aquatica, **355**, 822
latifolia, 823
miliacea, 822
Zoöspores, 461, 547
Zuni maize, **116, 120**
Zygomycetes, 462
Zygospore, 457, 496
Zygote, 469
Zymase, 137

J.R. 20/7/37

Bot. 207737
G.

Author Gager, Charles Stuart

Title General botany.

University of Toronto
Library

DO NOT
REMOVE
THE
CARD
FROM
THIS
POCKET

Acme Library Card Pocket
Under Pat "Ref. Index File"
Made by LIBRARY BUREAU